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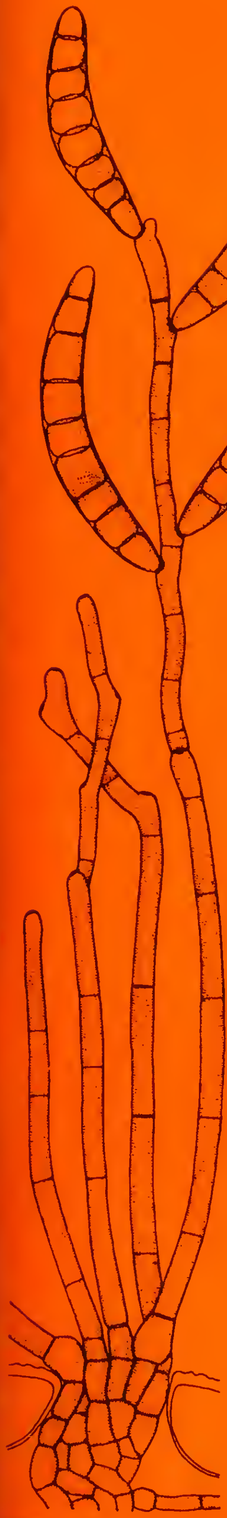

EPIMAY

A Simulator of Southern Corn Leaf Blight

P. E. Waggoner

J. G. Horsfall

R. J. Lukens

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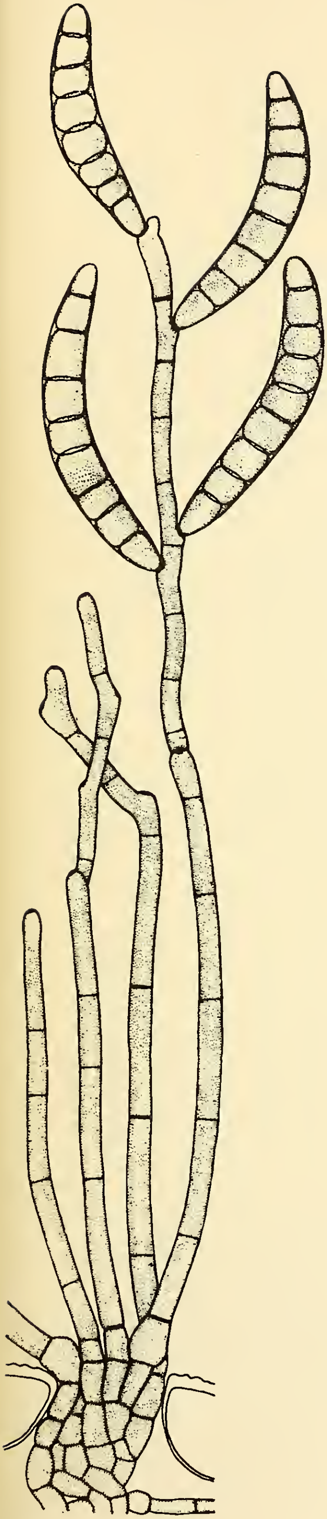

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Contents

INTRODUCTION ... 3
- A. The Nature of the Epidemic ... 4
- B. The Responses of *H. maydis* to Weather ... 5

I. EXPERIMENTS WITH HELMINTHOSPORIUM MAYDIS ... 7
- A. Materials and Methods ... 8
- B. Stalk Formation ... 9
  - Moisture ... 12
  - Temperature and Light ... 12
  - Effects of Rain ... 15
- C. Spore Formation ... 15
  - Succeeding Crops of Spores ... 20
- D. The Take-off ... 22
- E. Germination and Survival of Spores ... 22
- F. Penetration ... 24
- G. Infection Efficiency ... 26
- H. Enlargement ... 28
- I. Light and Susceptibility ... 30

II. INTEGRATING THE FUNGAL CYCLE AND WEATHER INFLUENCES INTO EPIMAY ... 30
- A. Reading the Weather Reports ... 31
- B. Fungal Character ... 32
- C. The First Day ... 33
- D. An Overview ... 35
- E. Stalks Are Formed ... 36
- F. Spores Appear ... 39
- G. Spores Are Washed Off Stalks by Rain and Caught by Leaves ... 40
- H. Spores Are Blown by Wind and Caught by Leaves ... 43
- I. Spores Germinate ... 44
- J. Germinated Spores Invade Leaves ... 45
- K. Infections Incubate ... 48
- L. Lesions Enlarge ... 48

III. THE REALISM OF EPIMAY ... 50

IV. EXPERIMENTS WITH THE CHARACTER OF PATHOGEN AND HOST ... 55
- A. The Leaf Area ... 55
- B. How the Pathogen Is Blown and Caught ... 56

V. EXHAUSTION OF THE HOST ... 57

VI. SYMBOLS ... 62

VII. CITATIONS ... 65

APPENDIX ... 67

The cover drawing is from E. S. Luttrell's paper in the American Journal of Botany 51(2): 214, 1964.

EPIMAY

A Simulator of Southern Corn Leaf Blight

Paul E. Waggoner, James G. Horsfall, and Raymond J. Lukens

The Great Epidemic of Southern Corn Leaf Blight of 1970 startled this nation that thought that its technology was able to protect its supermarkets from the vagaries of Nature. Perhaps more importantly, the Epidemic brought unease to a world still enjoying the euphoria of the Green Revolution. Plant breeding set the stage for the Epidemic, and plant breeding has already moved to solve the problem. Nevertheless, there was a task for the epidemiologist.

Since the blight pathogen is a fungus and like so many others is susceptible to the weather, it was our task to explore the effects of environment upon all stages of the pathogen in the laboratory and greenhouse during the winter and spring and then assemble the effects into a logical and epidemimetic simulator, match the response of the fungus to the weather, and thus reveal the likelihood of blight at different places in 1971.

We call this simulator EPIMAY to distinguish it from EPIDEM, which we developed a few years ago for the early blight disease of tomato and potato. EPIMAY was ready by June 1971, and the Weather Bureau and Purdue University and its associated Laboratory for Remote Sensing generously employed it in their important work that year (Felch and Barger, 1971). This Bulletin now reports the necessary experiments in environment and pathology, the composition of the simulator, and some early tests of its realism.

Since epidemimetic models are fairly new, a short illustration is in order for those whose science is other than model building. An epidemimetic model or simulator aims to "run like a real epidemic." It should mimic the epidemic; hence, the adjective epidemimetic.

The simulator is assembled from three components: weather as observations, the pathogen in the guise of a knowledge of how all its stages react to weather, and finally the computer program or instructions for presenting the current weather to the pathogen and asking how it would react. With these three parts of the simulator the computer calculates whether the epidemic rises, falls, or remains level.

As an example, the computer tells the simulated fungus that it is 3 in the morning on June 10 and hence dark. The temperature is 17 C, and the leaves have become wet with dew. In its capacious memory the computer has some census data about the fungus. There were 100 lesions on June 1 and a few more appeared on June 6, 7, and 8. It has calculated how large these lesions have grown and figures that they bear 120 microscopic sporophores or stalks. Most spores have been blown from the stalks during the preceding dry hours, and 80 have come to rest on healthy leaves. The computer now asks the simulated fungus, "What will happen during 3 hours?"

The lesions enlarge according to the temperature and their size. Since the leaves are wet, the lesions that are not yet coverd with stalks grow 58 thousand more. The leaves have not been wet long enough for sporulation to begin, and the dew prevents the flight of spores already formed. The dew does, however, allow 47 of the spores on healthy leaves to germinate. It also allows 5 to go on and penetrate or infect the leaves. And so as the weather changes hour by hour, the computer continuously asks the fungus what its responses are, and the answers are recorded. The simulated epidemic accelerates or slows accordingly.

A. The Nature of the Epidemic

The pathogen responsible for the southern corn leaf blight is a fungus called *Helminthosporium maydis.*

H. maydis has been around a long time. In 1925 Drechsler wrote that the fungus was "the cause of a destructive disease manifested by the appearance on the leaves of numerous dead cinnamon-buff or purplish areas surrounded by a darker reddish brown margin, and often delicately variegated with brownish zonate bands; the lesions longitudinally elongated, . . . typically limited to a single intervascular region, . . . often coalescing to form more extensive dead portions." He had found the fungus in Florida and the Philippine Islands in 1917 and 1918. Although he called the disease "destructive," a half century would pass before it was taken seriously.

During that half century farmers learned the virtues of hybrid corn economically produced by the double cross (Jones, 1918), and seedsmen learned the economies of producing the seed from female parents with pollen sterility that was restored in the progeny (Jones and Mangelsdorf, 1951). Most of the economies were passed on to the consumers: it made corn and the livestock that ate it cheaper.

The very merit of the hybrid corn system employing one strain of pollen sterility, the T type, set the stage for the epidemic, however. By 1970 the T type of cytoplasm had driven the competition from the field and was spread across most American corn fields. By 1968 the unimportant *H. maydis* had changed to a virulent pathogen that rotted a hundred tons of seed (Ullstrup, 1970, cited by Tatum, 1971). In 1969 the attack was noted in seed and test fields (Scheifele et al., 1970), and during the winter Hooker et al. (1970) confirmed the presence of a new T race of the pathogen matched to the wide spread T cytoplasm of the corn.

In 1970 the pathogen struck. Its ravages could be seen from the air as well as the ground, and the December estimate of the American corn crop was 15% less than the estimate before blight struck. Losses of half or more were common in fields throughout the Gulf region (Tatum, 1971). In years to come, economists will unravel just how much the epidemic cost the consumers of hamburger, both in America and overseas where imported American grain is fed to livestock. So much for the epidemic.

B. The Responses of H. Maydis to Weather

Our first task was learning how the fungus, in fact, does respond to different weather patterns. What factors are favorable and raise the rate of the epidemic? What factors are unfavorable and slow the rate of the epidemic? The first step, of course, was to examine what had been learned in the past.

Nisikado (1927) found that *H. maydis* on a laboratory medium produced most mycelium at 30 C and most spores at 23 C; the leaf spot disease was most severe at 30 C. Since maximum germination and penetration occurs within 18 hours following inoculation (Jennings and Ullstrup, 1957), 18 hours of wet leaves would be ample if—as one expects for many fungi—desiccation kills. Since Drechsler (1925) made his early observations of the disease in two warm, moist places, one does expect it will be favored by warm, moist weather. Wehlberg (1962) wrote about several pathogens of sweet corn leaves in southern Florida, including *H. maydis,* and said disease was severe during wet weather. This is all the information we have found about *H. maydis* and the weather. It is not enough to build a simulator, but we can already see that warmth and moisture will favor the disease.

Before we begin rectifying the paucity of information in the literature by entering the laboratory, we should, however, admit the complexity of the task and lay some plans for integrating the information in an orderly pattern. If we do not lay our plans carefully, we shall not know when we are collecting a plethora of irrelevancies and when we are overlooking missing links. Further, we shall go to a lot of trouble to collect a multitude of observations and then not be able to employ them easily. Our plan is disarmingly simple and will be recognized by readers who have seen the simulator of potato late blight (Waggoner, 1968) or EPIDEM (Waggoner and Horsfall, 1969).

First, the life cycle of the fungus is divided into the usual stages (Fig. 1). Leaving aside the arcane symbols until we need them later, we see that Fig. 1 simply says that the fungus produces sporophores or stalks that bear spores. These are carried in water or air to new hosts where they germinate and invade. During the incubation period the fungus grows in the host and produces new lesions. New stalks form on the lesions and the cycle is complete. How does the weather affect each of these stages? That must be explored in the laboratory and the greenhouse.

After the information is assembled into the simulator the number of fungal units in each stage will be calculated from the number in the preceding stage, from the weather, and from the rules that summarize the observed relations between the increase in each stage and the weather. Since we shall make our calculations as frequently as each 3 hours, we shall not have to worry about the complexities or interactions caused by the different environmental optima for different stages; this will be tended to by remembering how many individuals are in the preceding stage. Since we shall not consider the spread of disease between localities except to enter some inoculum to start the simulated epidemic and shall postpone

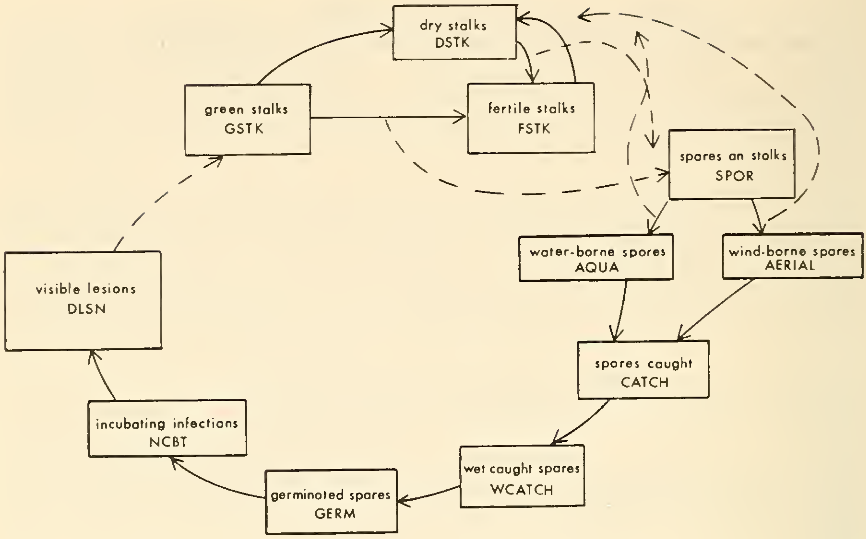


Fig. 1 The life cycle of *Helminthosporium maydis.*

considering the shortage of new hosts that occurs when most of the corn is diseased, the simulator EPIMAY will appraise whether the weather will favor or inhibit *Helminthosporium maydis* and southern corn leaf blight. In Chapter V we shall consider what happens when most of the corn is diseased and little new tissue is left for the fungus to invade.

The explanation of EPIMAY is aided by some general comparisons of simulation with other means of calculating the course of epidemics. The essential characteristic of a simulator is its logical assembly from parts that correspond to components of the real thing. That is, EPIMAY has parts that concern sporulation and so does the real epidemic. A simulator can be tested by testing its parts as well as the whole. It bridges the gap between the precise but unnatural laboratory and the imprecise but natural outdoors. It can be logically changed by changing its parts, for example, when changes in the virulence of the host or the resistance of the host change the number of spores per day or per lesion. It can also be logically changed when initial infection changes.

Simulation can be contrasted with calculation by a regression equation, such as Evermeyer and Burleigh (1970) obtained from historical observations of wheat leaf rust and weather in Kansas. Such a regression equation calculates the epidemic in the field in terms of past epidemics in the field. Since the regression equation has been derived from the very data that would be used for a test, it need not be tested. There are, however, no identifiable components, as sporulation, that can be taken from the laboratory. Lacking these components, the regression equation cannot be logically changed for changed virulence, resistance, or initial infection. Laboratory experiments can help the regression equation little.

Simulation can also be contrasted with a differential equation relating disease increase to disease extant (Van der Plank, 1963). The differential equation, of course, expresses the great generality that disease increases in proportion to the amount of inoculum and the amount of susceptible host, while the simulator concerns the effect of environment upon the change in each stage of the pathogen.

Finally simulation can be contrasted with a scheme for forecasting epidemics. Forecasting is, of course, a purpose and not a method of calculation. The scheme may be a regression equation, a differential equation, a set of threshold temperatures or humidities derived from field or laboratory, or even a simulator. Although a simulator may be used for forecasting, the simulator is also a guide for experiments, a test of our knowledge of physiology and a means for anticipating the significance of changes in the character of the host, pathogen or climate. It is now time to leave the generalities of the introduction and get down to the specifics of experiments.

I. EXPERIMENTS WITH HELMINTHOSPORIUM MAYDIS

Composing a simulator is an exercise in feedback from desk to laboratory and greenhouse, and back to desk. If the composer had at hand a full set of knowledge of *Helminthosporium maydis* and southern corn leaf blight, he could merely sit down at his desk, divide the life cycle of the fungus into stages, and write a set of rules that describes how each stage responds to weather and host. He would have a realistic simulator. This, of course, is not the way things really go. The composer's grand design is soon brought down to earth when he encounters gaps in his knowledge. Thus the exercise in feedback: the composer sets up the grand design of the fungal life cycle as shown in Fig. 1, tries to write the rules for the flow from rectangle to rectangle in the diagram, finds the parts that are missing, goes to the laboratory and gets those parts, progresses a little way around the diagram, encounters more ignorance, goes back to the laboratory again, and so on and on through weeks and months.

In many cases, of course, the ignorance cannot be replaced by fact because the composer simply is incapable of getting the missing piece. Then an assumption that he hopes is good sense must be fitted in. In many cases, however, the composer can get the needed information in the laboratory, and this chapter of our booklet reports these experiments that we needed and could make.

The subjects of our experiments can be related to the diagram, Fig. 1. We observed the effects of temperature, humidity, and light upon the formation of stalks. These stalks may be freshly formed or "green," or they may have been dried since their formation. We observed how fast these stalks became fertile or bore spores. We also observed the movement of these spores in water or upon the wind, their germination, their penetration or infection of tissue, the incubation of those infections, and finally the appearance of lesions on the plants. These experiments were performed as they were needed to compose a logical and realistic simulator, but they are presented first in our Bulletin so that the reader will have them at hand when the composition of the simulator EPIMAY is later presented.

A. Materials and Methods

We performed experiments in both the laboratory and greenhouse to measure the response of the fungus and the response of the host. Miss Barbara Wooding performed most of the experiments. Fortunately for us, she kept her eyes open and saw many things that were not in the experimental plans. For example, she discovered that a stalk had to form a branch before it could form a second spore after the removal of the first. Because she kept her eyes open, the simulator is more realistic.

The great southern corn leaf blight epidemic of 1970 was caused by Race T of *Helminthosporium maydis*. This race was successful because it prospered on the vast acreages of corn with Texas cytoplasm that populated America in 1970. The isolate of the fungus that we used was provided by A. L. Hooker of the Illinois Experiment Station. To him we are grateful. At first, we attempted to maintain the culture on potato dextrose agar, the gourmet diet of plant pathology, but this failed because the fungus lost its ability to produce stalks after two or three transfers. We then tried maintaining the culture on corn meal agar or even on Hopkin's synthetic medium (Nisikado, 1927). The fungus soon failed on these media, too.

Since we could not repeatedly subculture the fungus, we adopted a plan suggested by Perkins (1962). Sections of infected corn leaves were placed in a moist chamber and permitted to sporulate. Spores were collected from these leaves and transferred to potato dextrose agar and allowed to grow and cover about one-half to three-quarters of the plate. The mycelium and spores were then transferred to sterile silica gel in vials. The contents of the vials were then shaken, and the vials were stored in a refrigerator.

The next step in the procedure was required whenever inoculum was needed for an experiment. Some of the silica gel was dropped into a flask of casamino acid medium (Dimond et al., 1949). The flask was then shaken for 5 days. At the end of the 5 days, the mycelium grown in the 75 ml of medium was separated by decanting the fluid. The mycelium was then suspended in 80 ml of water in a Waring blender, ground for one minute, and then washed twice by centrifugation and suspension in water. The washed fragments of the mycelium were then suspended in 0.02 M phosphate buffer, pH 6.3. After the suspension was filtered through cheesecloth, it was spread over filter paper.

When spores were required to inoculate plants, the fungus was grown on the filter paper for 4 days in the light at 18 C, where it sporulated abundantly. The spores were washed from the paper into 100 ml of water and filtered through one layer of cheesecloth. The plants were then sprayed with the spores suspended in this filtrate until it ran from the leaves.

To study spore germination we required dry spores. These were obtained by first drying the mass filter paper culture and then brushing dried spores from the culture onto glass slides. Earlier, we had learned that spores would not germinate on new slides, and therefore, all slides were washed in dichromate solution. To moisten the spores on the slides, we sprayed them with ½% orange juice in double-distilled water.

So much for inoculum; now we describe the cultures or plants that were inoculated. In the case of culture on paper, the paper in a petri dish was simply inoculated and moistened by the mycelial fragments in 0.02 M phosphate buffer, pH 6.3.

Most of our experiments, however, were performed with the fungus growing on corn seedlings (PA602A, F1 hybrid). Two kernels were planted in soil in 600 ml paper cups. After 3 to 5 weeks the seedlings had four to five leaves and were ready for use. Occasionally we employed mature corn that had been grown in large crocks until silking.

The plants were grown, and sometimes incubated after inoculaton, in a greenhouse at about 21 C and without supplemental illumination. When a moist atmosphere was required, the cups containing the soil and the plants were enclosed in plastic bags. At other times the seedlings were simply incubated upon a laboratory bench at about 21 C and with normal illumination of the room.

Filter paper cultures, seedlings, or sections of leaf resting on moist filter paper in petri dishes were incubated in chambers. The temperature of these chambers was controlled within 1 C of the stated temperature. The chambers were illuminated by cool white fluorescent lamps and the illumination at the level of the culture was about 100 ft-c. When darkness was required the cultures were wrapped in opaque plastic.

B. Stalk Formation

The technical term for microscopic stalk that holds an asexual spore or conidium into the air above the leaf surface is "sporophore" or "condiophore," but the word "stalk" is just as clear, and it fits computer language better. The literature has surprisingly little to say about stalk formation, which is usually lumped with sporulation. Thus Nisikado (1927) tells us the temperatures that cause aerial mycelium and spores but does not separate the process of stalk formation. To build the simulator, however, we must separate the two processes because there will be no spores without stalks, and stalks like the weather to be warm whereas sporulation likes it temperate. Also stalk formation is often favored by light whereas sporulation may be favored by darkness.

The appearance of the stalks is described by Drechsler (1925). He said that stalks arise singly or in groups of two or three from stomata in the center of killed foliar parts, have septa at intervals of 15 to 60 microns, bear the first conidium or spore after attaining a length of 50 microns, and have points of attachment of successive spores marked by scars at intervals of 10 to 40 microns. He said that the stalks were 120 to 170 microns tall, but under moist conditions they were often taller than 1 mm.

Fig. 2 is a photograph of a stalk formed on filter paper in 24 hours. The stalk is composed of four cells and bears a spore. Fig. 3 is a view of diseased corn leaf showing a multitude of stalks, many of them growing from a vein

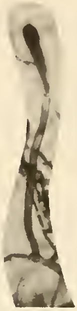


Fig. 2. Stalk and spore formed in 1 day on filter paper inoculated with mycelial fragments. Incubation at 23 C in light for stalks and then 5 hours at 20 C in the dark for spores.

and certainly not all growing from stomata. It is also evident in Fig. 3 that we saw fewer multiple spores than shown in Drechsler's drawings.

In Fig. 4 the development of stalks is shown in the upper half of the picture. The development of these stalks on filter paper after 2, 6, and 18

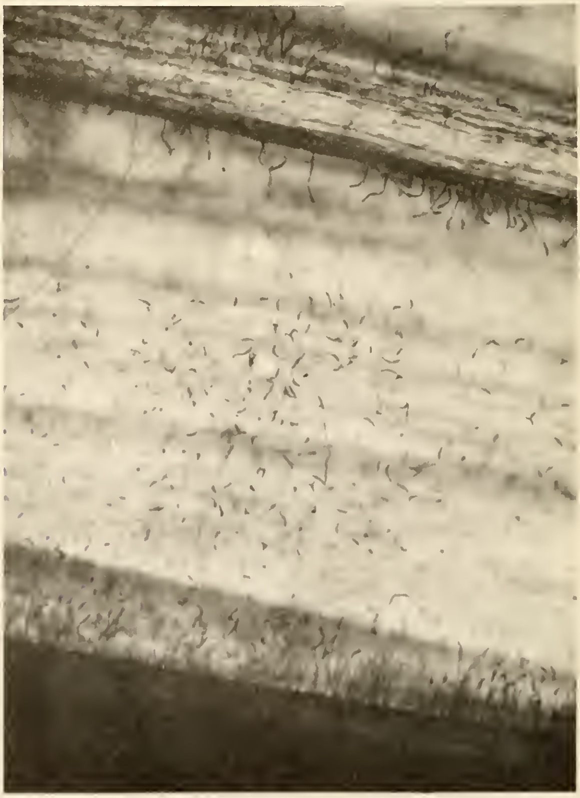


Fig. 3. Stalks growing from a leaf vein.

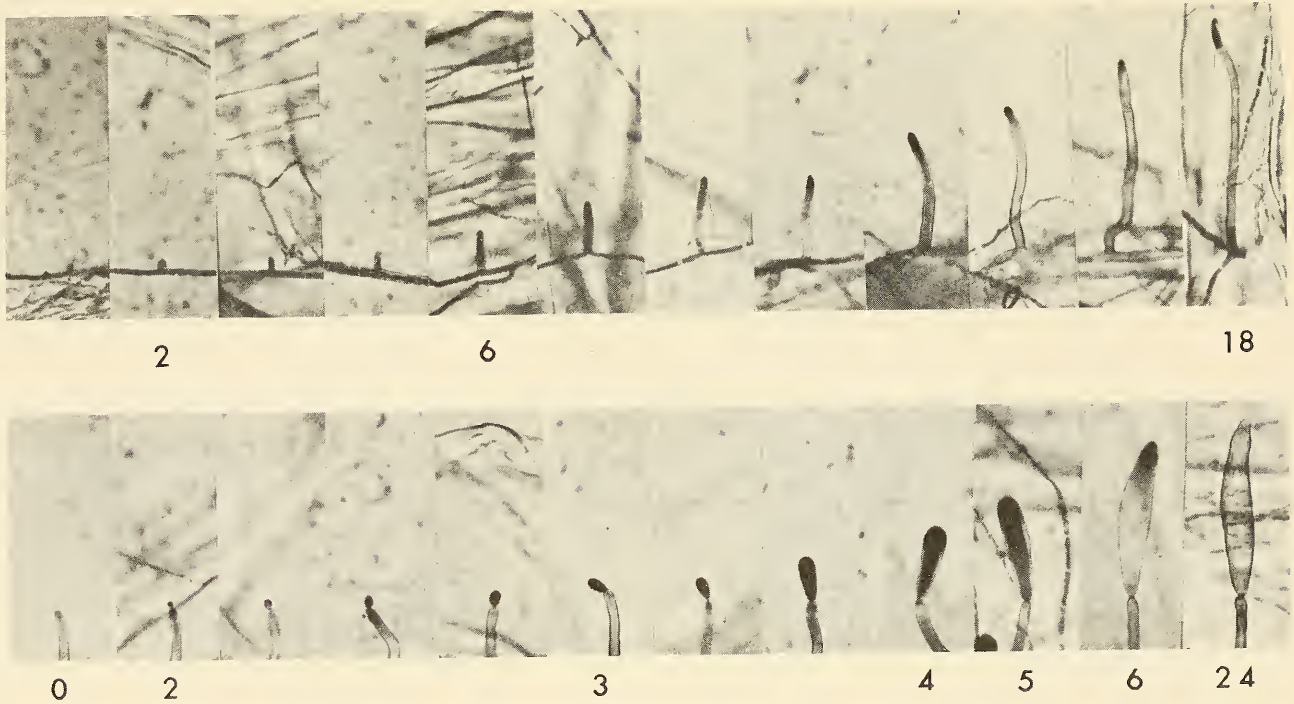


Fig. 4. The growth of stalks from 0 to 18 hours (top) and the growth of spores upon stalks from 0 to 24 hours (bottom).

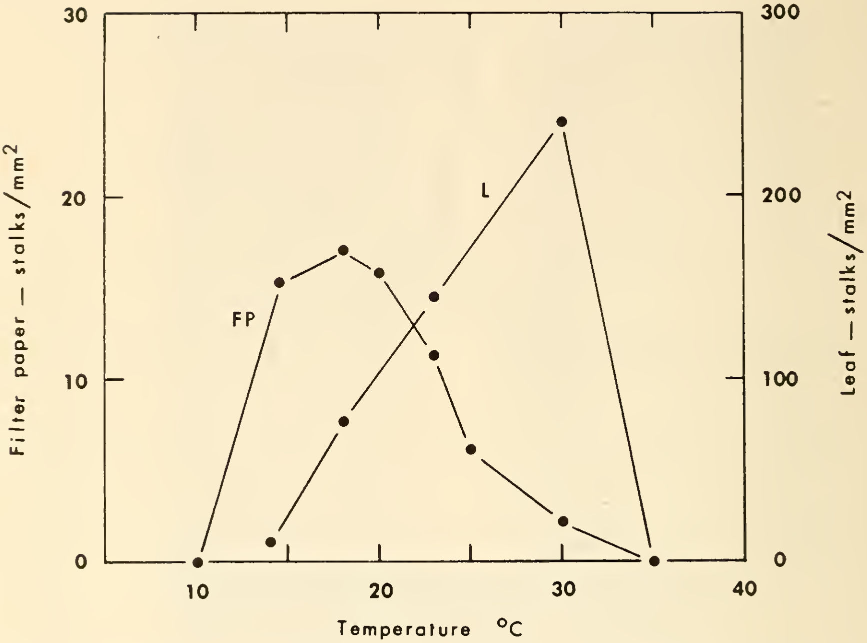


Fig. 5. The effect of temperature in the light upon the number of stalks/mm² 2 days after filter paper (FP) was inoculated with mycelial fragments or established lesions on leaves (L) were moistened. Experiments 1/6, 13, 2/9, 10, 23, 3/4, 4/13, 20.

hours is labeled. With this overview of the process at hand we can now describe the experiments in the effect of moisture, temperature, light, nutrition, and rainfall upon stalk formation.

Moisture: A moist atmosphere is required for stalk formation, even though the fungus is growing in a succulent leaf. In Experiment 3/17A corn seedlings were inoculated and kept moist for 24 hours. The leaves were then dried for a day. At the end of this day of drying, half the plants were enclosed in plastic bags. Five days later, that is seven days after inoculation, the plants in both moist and dry atmospheres had lesions of about the same size. Many stalks, and spores too, were seen on the lesions in the moist atmosphere, but no stalks had appeared on the lesions in the dry atmosphere. Thus the requirement of a moist atmosphere for stalk formation is clearly established, and we turn to the effects of temperature and light, which are more complex.

Temperature and Light: Our experiments on the effect of temperature and light upon stalk formation began with the simple medium of filter paper moistened with phosphate buffer. Two days after the inoculation of the filter paper with the mycelial fragments, the number of stalks on ten 0.74-mm² fields was counted on each of two plates. The number of stalks formed on paper in continuous light at the several temperatures is shown by curve FP in Fig. 5. It ranged from no stalks at 10 and 35 C to about 15 stalks per mm^2 at 14 to 20 C.

In our earlier experiments with *Alternaria,* we had found that nutrition affects stalk formation. Therefore in Experiment 4/27 we introduced different nutrition by dipping filter paper in casamino acid medium, (Dimond, et al., 1949), and then drying it. Subsequently, the filter paper was inoculated by mycelial fragments in phosphate buffer. After two days the number of stalks was observed. At 18 C there were twice as many stalks on the casamino acid medium as on the buffer alone, while at 23 C the two produced about an equal density of stalks. Clearly, the medium has a large effect not only upon the absolute number of stalks but upon the effect of temperature upon stalk formation. This means that a realistic simulator must employ information about stalk formation upon leaves and not upon an artificial medium.

The effect of temperature upon stalk formation on leaves in the light is shown by curve L in Fig. 5. The data were obtained from Experiments 4/13, 20 (This identifies experiments on April 13 and 20, 1971). Leaves had been inoculated three or four days earlier. Then sections were cut from leaves, and the infected leaves were placed in petri dishes on moist filter paper. After two days in the incubator, the leaves were removed, and the stalks per 1.63-mm^2 field were counted on two cultures. The data of the figures are averages of the two experiments. There is a marked difference in the effect of temperature upon stalk formation on a paper (FP) and on a leaf (L). Naturally, we must use curve L in the simulator.

In our earlier experiments with the closely related fungus *Alternaria,* we had observed a marked difference in the effect of temperature upon the fungus in the light and in the dark. Therefore, our next observations of stalk formation as it progressed through time were made not only at different temperatures but also in the light and dark. Fig. 6 shows the course of stalk formation. The observations at 2 days in the light have already been described. Observations of development in the dark at 2 days were obtained in the same fashion except the petri dishes were wrapped in opaque plastic. The data points at 1 day in Fig. 6 represent earlier observations upon the same material.

The next task is obtaining observations of stalk formation at times earlier than one day. Since such observations were not taken in the two Experiments 4/13, 20, stalk formation within the first 24 hours after placing the lesions in moist chambers was observed in Experiment 3/31A. At 23 C in the light, stalk formation on two or four leaves that had no stalks at 0 hours averaged 10 per mm^2 at 6 hours, 80 at 12 hours, 110 at 18 hours, and 140 at 24 hours. Thus in Fig. 6, we established a data point at 6 hours at a stalk density of a tenth the density observed after 24 hours.

The curves are extrapolated from day 2 to 3 in Fig. 6. This is justified by Experiments 2/23, 3/4, where stalk formation on filter paper proceeded regularly from day 2 to 3, partially by the formation of multiple stalks. In composing the simulator, the course of stalk formation from day 2 to

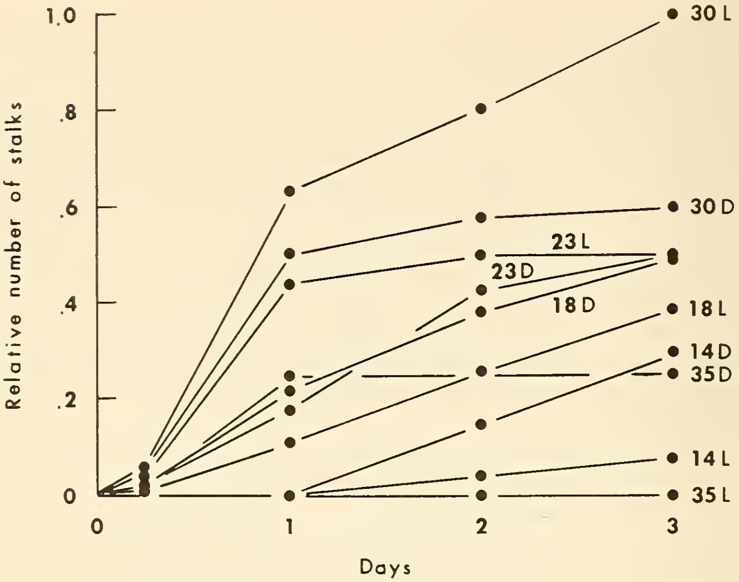


Fig. 6. The course of stalk formation on lesions at several temperatures in the light (L) and dark (D). Relative number is stalks/mm^2/300. The points at 1 and 2 days are observations of Experiments 4/13, 20. The points at 6 hours were set at a tenth of the 1-day values in conformity with Experiment 3/31A. The points at 3 days are extrapolations. The course of stalk formation used in the simulator.

3 will be of little importance because periods of moisture longer than 48 hours are rare in nature.

Eventually, we shall want to know the maximum number of stalks per mm^2. This is estimated to be 300 because there were an average of 240 per mm^2 at 30 C in the light at 2 days, Experiments 4 13, 20. The highest density among the four replicates was 290. Thus the extreme or maximum value of 300 is reasonable, and the ordinate "relative number of stalks" of Fig. 6 means relative to 300 per mm^2.

Before leaving the subject of temperature and light, a brief summary of the course of stalk formation on leaves is in order as well as a comparison of these courses with those of *Helminthosporium* and *Alternaria* on filter paper. In the realistic circumstances of *Helminthosporium* on corn, stalk formation is more rapid in the light than in the dark at 30 and 23 C, while at 14, 18, and 35 C light is detrimental to stalk formation. This detrimental effect of light at the cool and hot temperatures is in marked contrast to the course of stalk formation by *Alternaria* on paper (Waggoner and Horsfall, 1969); there, light was advantageous at 15, 23, or 27 C. Similarly, in six Experiments (1 6, 13, 2 9, 10, 23 and 3 4) stalk formation by *Helminthosporium* upon filter paper was always greater in the light than in the dark from 14 to 30 C. Thus, when we come to build our simulator, we shall use the more realistic course of stalk formation on lesions

(Fig. 6) and suspect that we may have found something much like this with *Alternaria* had we grown the fungus on leaves rather than on paper.

The effect of prior temperatures upon stalk formation was explored in Experiment 3/9. When filter paper was inoculated with mycelial fragments and incubated for a day at 18 C in continuous light, 12 stalks formed per mm^2. If the paper culture were incubated at 10 or 35 C, on the other hand, stalks did not appear even after 3 days. Now, what is the effect of a history of 10 or 35 C upon subsequent stalk formation at 18 C? When the moist filter paper cultures were incubated for 1 to 2 days at 10 or 35 C and then placed in light at 18 C for a day, there were only 4 to 8 stalks per mm^2. This is about one- to two-thirds of the stalks observed when the filter paper cultures were immediately placed at 18 C. Thus 10 or 35 C do not kill the mycelial fragments, but the hot or cold temperatures do inhibit subsequent stalk formation of paper. We have not explored the effect of prior temperature upon stalk formation on lesions, nor have we incorporated this observation into our simulator. It remains a subject for further investigation.

Effect of Rain. Up to this point we have been considering the increase or growth of stalks, but we must now consider their destruction. For example, in the next section, the reader will learn that drying inhibits or slows the formation of spores upon the stalks, but does not kill them. In this final section on stalks, on the other hand, he will learn how a rain beats down the existing stalks and prevents spore formation on some. In Experiments 3/17B, 6/3 filter papers were inoculated with mycelial fragments, and stalks formed during the subsequent 2 days in the light at 23 C. Sporulation was then induced by incubating the plates in the dark over night. Eighty-one and 95% of the stalks had spores in the two experiments. The filter paper culture was then subjected to ¼ inch of simulated rain by sprinkling it with water. The cultures were returned to the dark overnight and had only 60 and 50% re-sporulation the next day. Thus, a quarter inch or 6 mm of rain reduced the number of stalks capable of producing spores by a half to a quarter. This is not surprising, since the stalks were flattened by the rain. In the simulator we shall assume that a quarter-inch rain destroys a quarter of the stalks.

C. Spore Formation

The literature is not replete with information on spore production by *H. maydis*, but it does provide more information on spore than on stalk production. We must, however, beware of this information because spore production is often confounded with stalk production. In our experiments, we have tried to separate the two processes by one of two devices. Either we began our experiments with stalks formed in light at 23 C, which inhibits spore formation, or we measured sporulation as the per cent of stalks with spores.

The appearance of the conidia or spores was described and, of course, depicted by Drechsler (1925). He tells us that spores develop at 25 C on diseased leaves in damp chambers or on artificial media, measure 30 to

115 microns in length by 10 to 17 in diameter, are often strongly curved and usually widest near the middle, have rounded ends, and have a broad but inconspicuous basal scar. In our Experiment 6/24, spores grown on paper averaged 14 by 79 microns.

Many years ago Nisikado (1927) observed the effect of temperature upon *H. maydis*, which he had first described. He grew the fungus for 6 days on rice decoction agar and found no spores at 8 or 35 C, few at 11 or 33, and most at 23.

Our experiments began with cultures on filter paper. In Experiments 2/19, 24, 4/7 the inoculated filter paper was incubated at 23 C in the light, permitting the growth of stalks without sporulation. Thirty-one hours after an inoculation, abundant stalks had formed, and the plates were placed in the dark at a variety of temperatures. On the next day the percentage of the stalks with spores was counted on 50 stalks per plate on each of two plates per treatment and experiment. The average sporulation is shown in Fig. 7, curve FP. The maximum sporulation was at about 20 C and practically no spores formed at 4 or 30 C.

The sporulation percentage in Experiments 2/19, 24, 4/7 was obtained by pre-forming stalks. In Experiments 1/6, 13, 2/9, 10, 23, 3/4 we obtained much the same results by merely growing stalks and spores at the same time and observing the percentage of those currently formed stalks that bore spores.

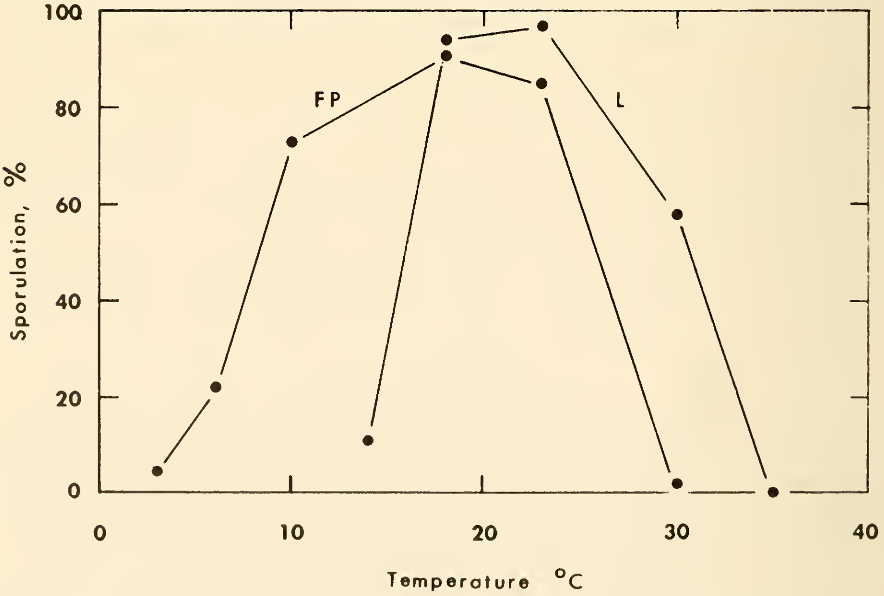


Fig. 7. The effect of temperature in the dark upon sporulation on filter paper (FP) and lesions (L). Stalks were pre-formed on FP for 1 day at 23 C in the light and then incubated overnight in the dark at the various temperatures. Established lesions L were incubated for 2 days in the dark at the various temperatures. Experiments 2/19, 24, 4/7, 13, 20.

In our experiments with stalk formation we obtained markedly different results when we used leaves instead of filter paper media. Therefore, we also studied sporulation on leaves. In Experiments 4/13, 20, leaf sections were placed in moist petri dishes and incubated in the light and dark. When the percentage of the stalks with spores after two days in the dark was observed on one 1.63 mm^2 field on each of two cultures per experiment and temperature, the curve L in Fig. 7 was obtained. On leaves the temperature optimum is fully 23 C and spores are rare below 10 or above 35. The reader will recall that Nisikado (1927) observed much the same outcome many years ago.

Since leaves are the most realistic medium for our simulator, we extended the Experiments of 4/13, 20 to include a variety of light and temperature combinations. The percentage sporulation at the end of 1 and 2 days is tabulated in Table 1. The most dramatic difference between light and dark is observed at 30 C.

Since moist periods will not often be as long as 24 hours, we must know something of the course of sporulation within the first day. This course of sporulation at shorter times was measured in Experiments 3/23, 30. Stalks were pre-formed on filted paper in the light at 23 C. They were then placed in the dark at 20 C and sporulation increased as shown in Fig. 8. The percentage sporulation was observed by counting the number of spores on 50 stalks in each of two cultures at each time. At 3 hours there were practically no spores, and at 6 hours the sporulation had reached a maximum. This maximum in Fig. 8 of about 90% is close to the percentage of sporulation at the end of 24 hours at 18 or 23 C in the dark, Table 1. Therefore, we conclude that when stalks are constantly wet they form practically no spores in 3 hours, but by the end of 6 hours they have attained a maximum sporulation shown in the column for 1 day in Table 1.

Since stalks will often dry in the field before they sporulate and we must relate our simulator to these real conditions, we next studied the course of sporulation on stalks that had dried. In Experiment 3/31 stalks were pre-formed on lesions at 23 C in the light. At the end of 24 hours, stalks were abundant and only 16% bore spores. The plates were then opened to the dry air of the laboratory and allowed to dry for one hour. At the end of the hour, they were again covered and placed in the incubator at 20 C in the dark. At 6-hour intervals the spores and stalks on a 1.63 mm^2 area of two or four leaves were counted. There were 200 to 400 stalks in the fields, and the percentage sporulation increased more or less linearly as shown in Fig. 9. When the stalks had been dried, they sporulated much more slowly than the continuously wet ones of Fig. 8. Nevertheless, at the end of 24 hours, they had reached about the same level of sporulation as the continuously wet ones of Table 1.

The course of sporulation can now be summarized by distinguishing between stalks that are continuously wet, which we shall call "green," and once-dried stalks, which we shall call "dry." The green stalks have practically no spores at 3 hours and have a maximum sporulation at 6 hours.

Table 1. Sporulation on lesions incubated in moist petri dishes. Experiments 4/13, 20

Temperature C	Light or Dark	Sporulation, % 1 day	Sporulation, % 2 day
14	L	0	25
	D	0	11
18	L	73	88
	D	89	94
23	L	17	47
	D	81	97
30	L	0	0
	D	33	58
35	L	0	0
	D	0	0

The maximum at 6 hours is the same as the number of spores at 24 hours, Table 1.

The dry stalks sporulate more slowly. Their more complicated course of sporulation is set out in Fig. 10, which is constructed in the following fashion. Since there are practically no new spores at the end of 6 hours (Fig. 9), sporulation for all conditions is set at zero at 6 hours in Fig. 10. Since sporulation on the dry stalks thereafter increases more or less linearly to the end of 24 hours (Fig. 9), straight lines are drawn between 6 and 24 hours or 1 day in Fig. 10. Since the level of sporulation on once-dried stalks at the end of 24 hours was about the same as on continuously wet stalks,

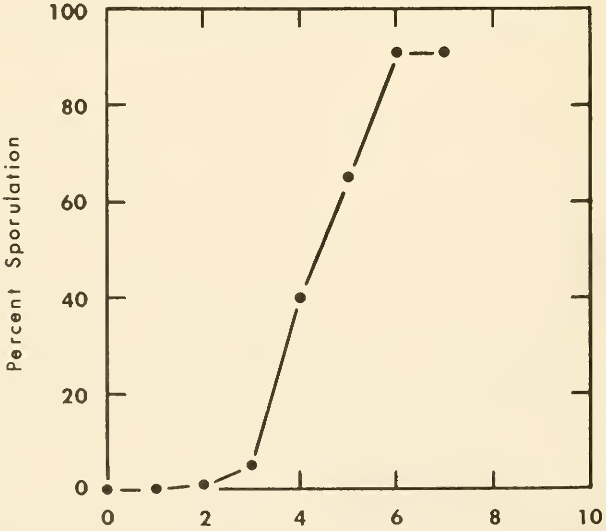


Fig. 8. The course of sporulation on pre-formed, continuously moist stalks on filter paper at 20 C in the dark. Experiments 3/23, 30.

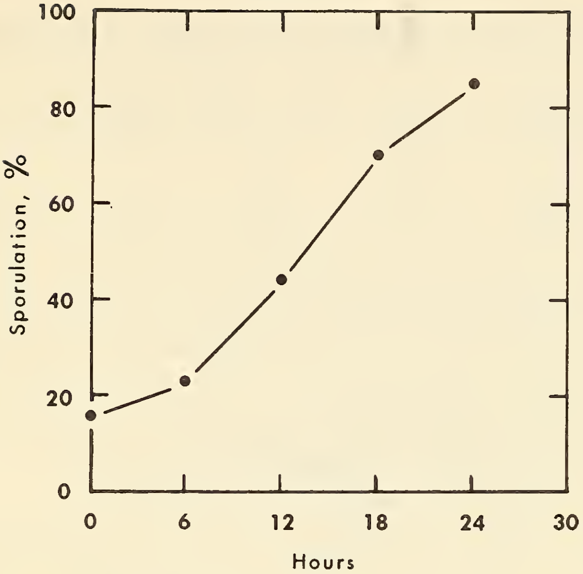


Fig. 9. The course of sporulation on pre-formed stalks on lesions. The stalks were dried for 1 hour and then incubated in a moist atmosphere at 20 C in the dark. Experiment 3/31.

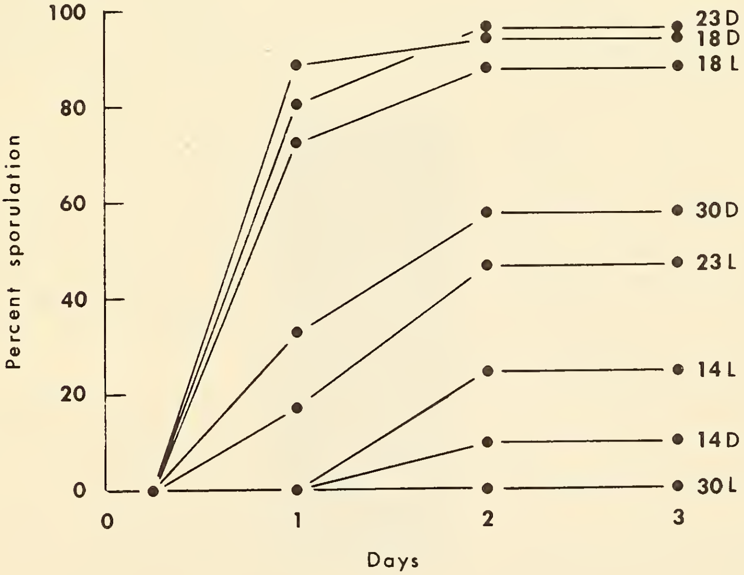


Fig. 10. The course of sporulation on once-dried or "dry" stalks used in the simulator. This is a composite of Fig. 9 and Table 1 as explained in the text.

Table 2. The formation of stalks and multiple spores on paper at 18 C in the light. Experiment 3/16

Day	Stalks/ mm^2	Spores/stalk, %				
		0	1	2	3	4
1	10	81	19	0	0	0
2	13	17	76	6	1	0
3	14	8	52	35	4	1
4	16	5	40	34	18	3

the level of sporulation for dried stalks after 24 hours in Fig. 10 is taken from Table 1. The level at the end of 2 days is also taken from Table 1. We assume that there is no further sporulation between 2 and 3 days; this last is a relatively unimportant point in the field epidemic because moisture will rarely persist more than 2 days.

The preceding summary describes the data that we shall incorporate into EPIMAY. We do, however, have data from Experiment 3/16 on the subject of multiple spores on a single stalk. Although these data have not been incorporated in EPIMAY, they will undoubtedly prove useful in the future, and we report them here. Filter papers were inoculated with mycelial fragments on day 0. They were then incubated at 18 C in the light, and the number of stalks and the proportion of them with different numbers of spores were observed in ten 0.74-mm^2 fields on each of two cultures. Table 2 shows that at the end of 1 day the cultures had an average of 10 stalks per mm^2. Of these stalks, 19% had one spore per stalk, and none had more than one. In other words, sporulation was 19%. This 19% is unaccountably less than the 70% of curve 18L at one day on Fig. 10. The Table shows that at the end of 2 days 76% of the stalks had one spore, 6% had two, and 1% had three spores. In our earlier experiments we would have called this 76 + 6 + 1 or 83% sporulation, even though 100 stalks bore 91 spores. Moisture will usually not persist in nature longer than 2 days but the events of the third and fourth day are interesting. The Table shows that by the end of the fourth day about half the stalks bore more than one spore. In summary, multiple spores do form on stalks especially after three or four days of continuous moisture, but for the periods of continuous moisture of less than 2 days, which will generally interest us in the simulator, we can call the percent of stalks with spores equal to the number of spores per 100 stalks without any serious error.

Succeeding Crops of Spores: Before leaving this subject of sporulation to study or explain the takeoff of spores, we need to know whether the takeoff destroys the stalks or permits successive crops. We shall want to decide whether the denuded stalks re-sporulate as rapidly as green ones or as slowly as dry ones sporulate. The green ones, the reader will remember, attained 90% sporulation in 6 hours whereas the dry ones only added 7%. In Experiment 4/14 stalks were formed on inoculated filter paper by incubating them at 23 C in the light. They were then caused to sporulate by incubation at 20 C in the dark. The spores were blown away by huffing and puffing at them with a syringe. The cultures were then incubated for

6 hours in light or dark at the three temperatures shown in Table 3. The percentage sporulation at the end of 6 hours, which is shown in the Table, shows that re-sporulation is more nearly like the slow process on dry stalks than like the rapid process on green stalks. The reader will later find we take this into account in EPIMAY by calling the denuded stalks dry stalks.

Miss Wooding noticed a phenomenon that probably explains the slow re-sporulation of the denuded stalks. Fig. 11 shows a spore formed on a stalk from which an earlier one had been blown. There is a small crook about two-thirds of the way up the stalk. This is where the first spore was born. After it was removed, the stalk formed an extension upon that earlier

Table 3. The speed of re-sporulation upon stalks after the first spores are removed by blowing or washing. The sporulation after 6 hours on "green" and "dry" stalks is included to show re-sporulation resembles sporulation on "dry" more nearly than on "green" stalks. Sporulation is the percent of stalks with spores after 6 hours.

Temperature C		Light or Dark	Sporulation, %	Experiment
20	Green Stalk	D	90	3/23
20	Dry Stalk	D	7	3/31
18	Blown	L	20	4/14
		D	10	
23	Blown	L	4	4/14
		D	30	
30	Blown	L	0	4/14
		D	0	
20	Washed	D	0	6/3

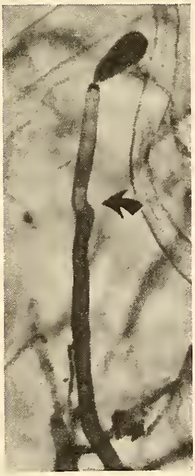


Fig. 11. Re-sporulation on a stalk denuded by wind. The first spore, which was blown away, was borne at the crook about two spore lengths below the present spore. During the following 24 hours a branch and hence the crook was formed; then a new spore appeared.

stalk and finally formed a spore upon this. Thus it is not surprising that re-sporulation on denuded stalks is slower than on green stalks, requiring us to classify denuded stalks as "dry" ones.

Next we observed the course of re-sporulation on stalks whose first spore had been washed away by a simulated quarter-inch rain. In Experiment 6/3 spores were removed from stalks by the simulated rain. No spores had appeared at the end of 3 or 6 hours after this rain. At the end of 24 hours half the stalks had grown spores. Thus when spores have been washed away, we must certainly classify the stalks as dry stalks with a slow rate of sporulation rather than as wet ones that can produce 90% sporulation in 6 hours. As in successive sporulation on stalks that had lost their spores in the wind, growing an extension of the stalk as well as a spore was required and visible when spores had been washed away.

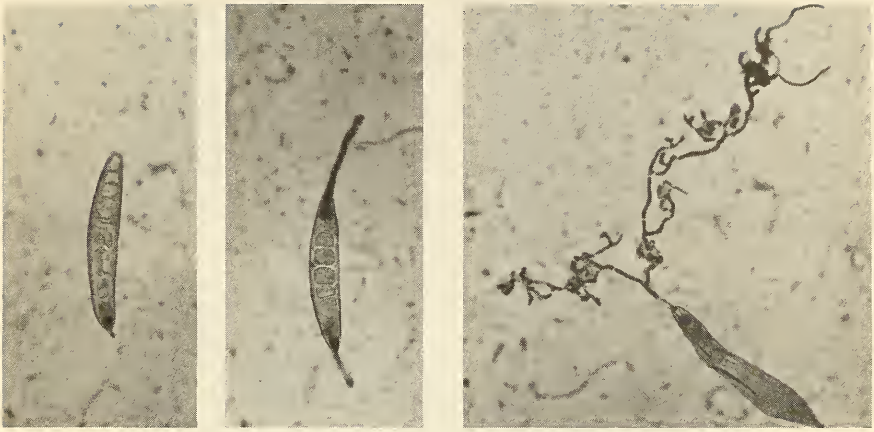
D. The Take-off

The blowing of spores from stalks by the wind was simulated by puffing at a culture on paper with a syringe held 25 to 35 mm from the paper. This removed all the spores. On the other hand, when the syringe was held 50 mm from the lesion, only about half the spores were removed. This simple Experiment 3/17 tells us that winds will remove spores and that removal will change with wind speed. The removal of spores by rain was also studied in Experiment 3/17. A drop of water falling from a medicine dropper held 6 or 25 mm above a filter paper culture knocked the spores from the stalks to the filter paper below, essentially removing all spores from stalks within its range. The conclusion from this simple experiment is that spores are washed from the stalks by rain. It seems sensible that the washing will increase, but not indefinitely, with the amount of rain. Kenneth (1964) performed similar experiments with wind and water with other species of *Helminthosporia*, and the outcome was the same.

E. Germination and Survival of Spores

Since spores of the related genus *Alternaria* germinate in humid air (Munnecke et al., 1959), we placed *Helminthosporium maydis* spores on glass slides above sulphuric acid solutions that created humidities of 70, 81, 85, 89, 94 and 100% relative humidity. At the end of 24 hours there were small germ tubes on spores at 70 and 95% relative humidity, but only at 100% were there extensive germ tubes (Fig. 12). At 100% relative humidity, droplets of water had formed on the slides. From these Experiments 3/9A, 12, we conclude that *H. maydis* spores differ from those of *A. solani*. *H. maydis* spores germinate poorly unless they are in water.

The next task is observing the course of germination in water at a variety of temperatures. In Experiments 2/25, 3/3, 5, 11, 5/11, 6/22 we observed the percentage of germination over a period of about 2 days. The results are depicted in Fig. 13 and 14. Clearly 23 C is the optimum temperature for germination, 10 C nearly stops germination, and 40 C does stop it. In the early experiments germination was rapid at 35 C and the



70 94 100

Fig. 12. The effect of humidity upon germination for 1 day at 23 C. The relative humidities are shown along the lower margin.

computer simulation will use a more rapid germination at 35 C than is indicated by Fig. 13.

The last concern about germination is the survival of the spores once they have been wetted and put out their germ tubes. In Experiments 3/9 B, 3/11 A spores were germinated in depression slides contained within the moist atmosphere of a petri dish. At the end of 4 hours many of the spores

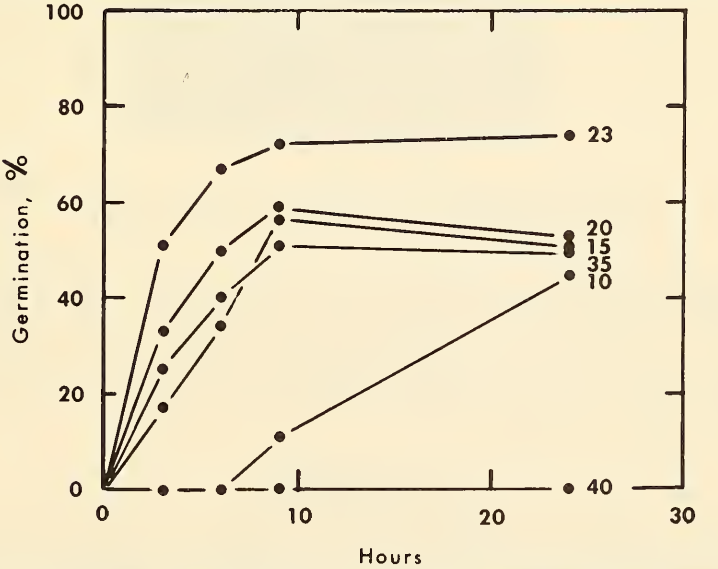


Fig. 13. The course of germination at several temperatures. Experiments 2/25, 3/3, 5, 11, 5/11, 6/22.

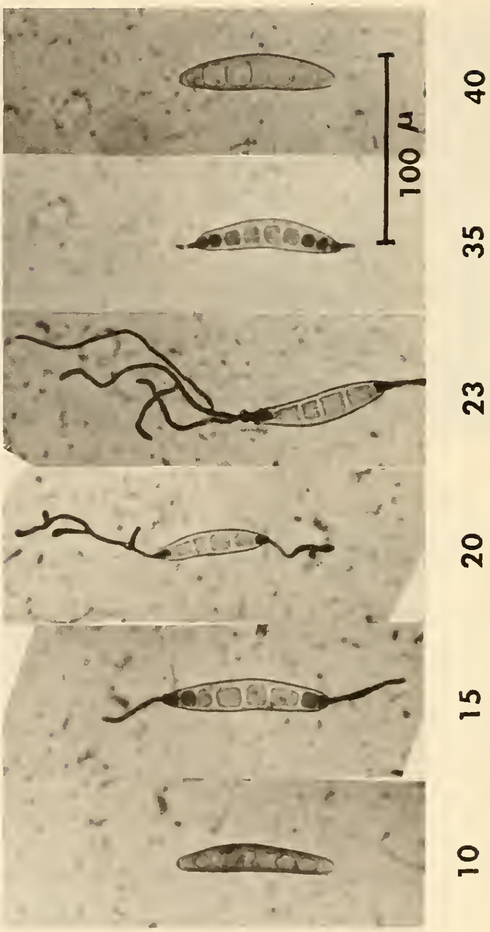


Fig. 14. The effect of temperature upon germination for 3 or 4 hours. The temperatures are shown along the lower margin.

had germinated, and the top of the petri dish was removed. Within about 15 minutes the air of the laboratory dried the solution in the depression. When the cover had been off the chamber for fully 2 hours, the spores were rewet and the chamber closed. No further growth was observed, indicating that the drying of germinated spores killed them, just as it killed *Alternaria* spores that had germinated.

F. Penetration

The germ tubes of *H. maydis* form appressoria on the cuticle of leaves. An appressorium is a flattened body from which the fungus punches an infection peg into the host. Hence, the formation of appressoria was observed. Fig. 15A shows appressoria formed very near the spore, while

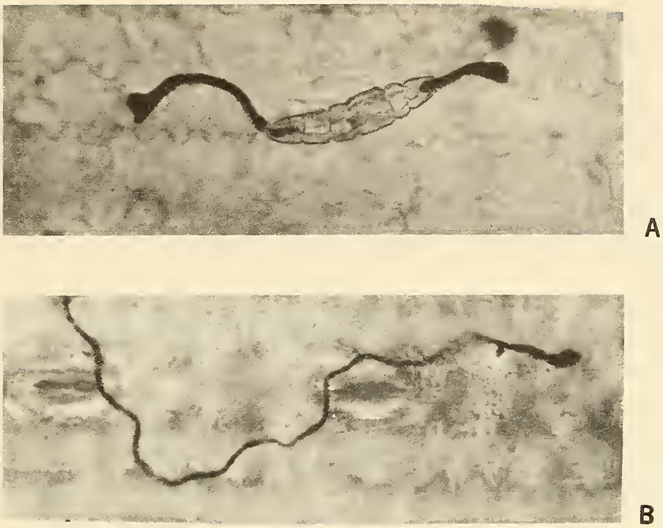


Fig. 15. Appressoria on a leaf.

Fig. 15B shows an appressorium formed at the end of a long germ tube that had by-passed two stomata.

The effect of temperature upon appressoria formation is shown in Fig. 16. Clearly 23 C is the optimum for appressoria formation as it was for germination. On the other hand, although 15, 20, and 35 C permit abundant germination, these three temperatures permit few appressoria to form in 6 hours. If appressoria are important in penetration, then there should be little penetration at cool and warm temperatures even though germination is possible there.

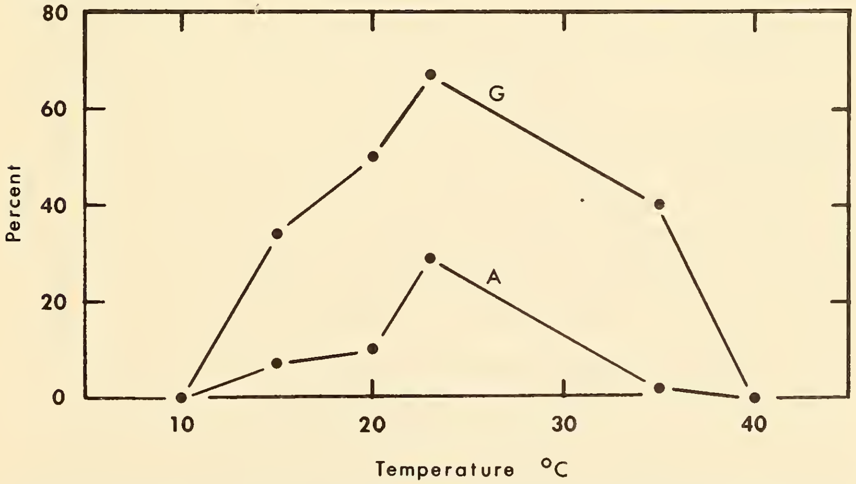


Fig. 16. The effect of temperature upon germination (G) and appressoria (A) formation in 6 hours. Experiments 2/25, 3/3, 5, 11, 5/11, 6/22.

The total process of penetration was observed in Experiments 3 10, 17C, Fig. 17. Seedlings were inoculated with a spore suspension; they were then placed in plastic bags. After 0, 3, 6, 9, 12, 24, and 48 hours of incubation in the laboratory at 25 C two cups containing two seedlings each were removed from their plastic bags. Two days after inoculation the numbers of lesions on three leaves of each seedling were counted. Fig. 17 shows the regular increase in the average number of lesions per leaf as wetness was prolonged up to 24 hours. There was no further increase between 24 and 48 hours.

The effect of temperature upon penetration was explored in Experiments 4/5, 15, 5/3. Fig. 18 shows that penetration was most rapid and successful at 23 C as the formation of appressoria predicted. Penetration at 18 and 30 C, however, is considerably less, probably because few appressoria formed at those temperatures. When we come to write the simulator we shall employ a much slower penetration at 18 and 30 than at 23 C in order to provide for less penetration and equal germination at 18 and 30 relative to 23 C.

G. Infection Efficiency

Before the number of lesions can be calculated from the number of spores, the number of spores required to produce one lesion must be learned. Fig. 17 shows how the number of lesions per leaf increases with duration of moisture, but we have yet to discover how many germinated spores were applied per unit area to produce those lesions. The proportion of spores that produce lesions under optimum conditions is the "infection

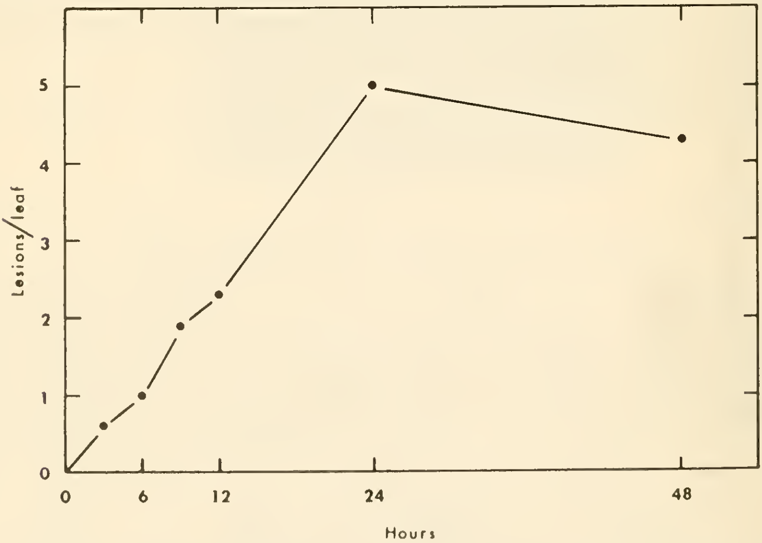


Fig. 17. The number of lesions per leaf following 0 to 48 hours of incubation at 25 C in a moist atmosphere after inoculation. The plants were exposed to dry air after this incubation, and the lesions were counted on all plants 48 hours after inoculation. Experiments 3/10, 17C.

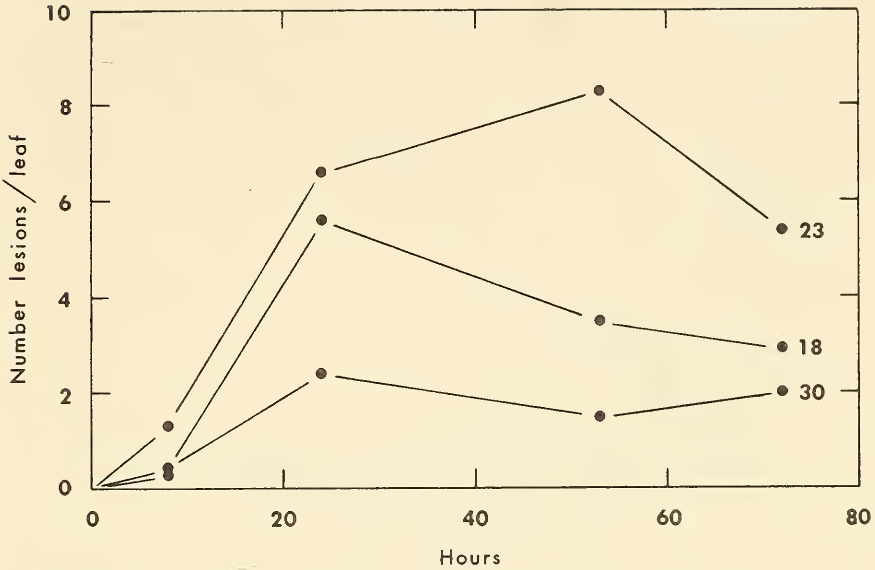


Fig. 18. The number of lesions per leaf following 0 to 72 hours of incubation at 18, 23 or 30 C in a moist atmosphere. Afterwards the plants were incubated in dry air at 25 C, and the lesions were counted 6 days after inoculation. Experiments 4/15, 5/3.

efficiency" (Gregory, 1961). Since the number of germinated spores will be calculated before calculating infection, the infection efficiency that EPIMAY will require is the ratio of lesions to germinated spores rather than all spores.

In the first experiment on this subject, spores were pipetted onto leaf sections. Since the difficulty of wetting the leaves made the distribution of the suspension uneven, this method was abandoned.

In Experiments 7/15, 20, spores were dusted onto leaves. Sections measuring about 3-by-7 cm were cut from leaves of seedlings and placed in moist petri dishes. Then different quantities of spores were brushed from filter paper cultures onto the leaves. After a day or two the leaves were examined under the microscope, and the number of germinated spores and small lesions were counted. The densities of germinated spores varied from 2 to 118 per cm^2, and the densities of lesions varied from 1 to 23. Fig. 19 shows that the infection efficiency was 0.2, regardless of the densities of spores.

The 0.2 efficiency is among the greater ones reviewed by Gregory (1961). The large 0.2 is not surprising, however, since failures in several steps of the cycle of the pathogens have been included in some of the earlier efficiencies, while we have observed spores actually resting and germinated upon the leaf for the calculation of the 0.2 efficiency of *H. maydis*. Thus the conclusion is: after all the losses in dispersal and germination have

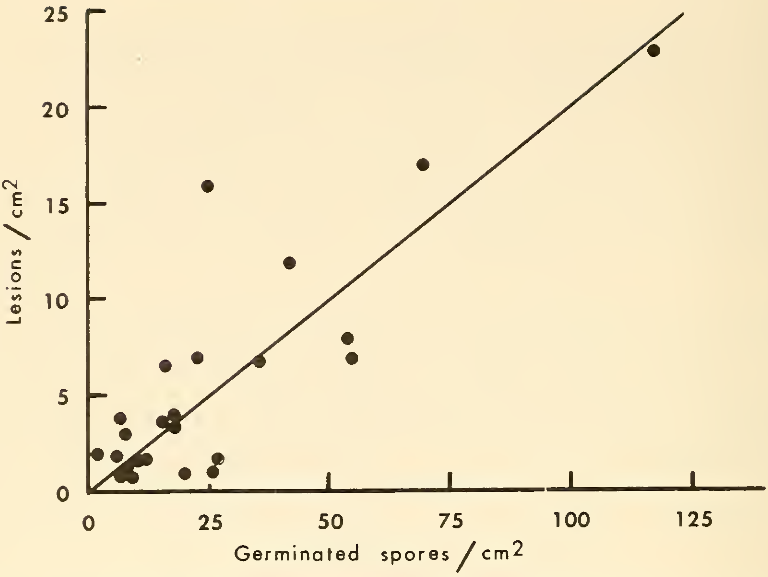


Fig. 19. The lesions produced on moist leaf sections by diverse densities of germinated spores. Experiments 7/15, 20.

been considered, still only about one spore in five can produce a lesion in optimum conditions.

H. Enlargement

To calculate the number of stalks that form on a new lesion that is the offspring of a spore we shall want to know how soon the lesion appears, how large it grows, and how much of its area is covered by stalks. First, how soon do lesions appear? We have just said that we counted small, pinpoint lesions in 2 days. However, stalks are absent from lesions 3 days after inoculation, become apparent in 4 days and are abundant in 5 days. Later, when we compose the simulator we shall use an incubation period of 3 days.

The next subject was the enlargement of the lesion area. In Experiments 3/17 A, 17 D, 22, 4/13, 20, plants were inoculated, kept moist for 24 hours, permitted to dry for a day, and then placed in a moist atmosphere in incubators at several temperatures. The areas of brown lesions were measured on two to five plants at each temperature in each experiment at daily intervals. The rapid expansion of lesions at 30 C and the slower expansion at 10 and 35 C is clear in Fig. 20. Since the lesions did not expand between days 4, 5, and 6 in Experiment 3/26, it is reasonable to set a maximum size, 87 mm^2.

Although the plants of Fig. 20 were kept moist, we also learned in Experiment 3/17A that moisture had no visible effect upon the enlargement of the lesions. In that experiment bagged and unbagged plants were kept at 25 C, and the lesions on both enlarged at about the same rate, Fig. 21.

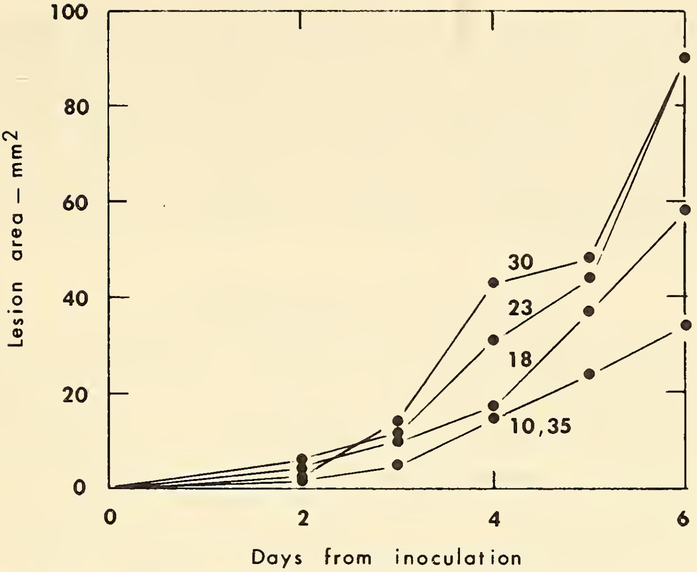


Fig. 20. The enlargement of lesions at several temperatures in a moist atmosphere. Experiments 3/17A, 17D, 22, 4/13, 20.

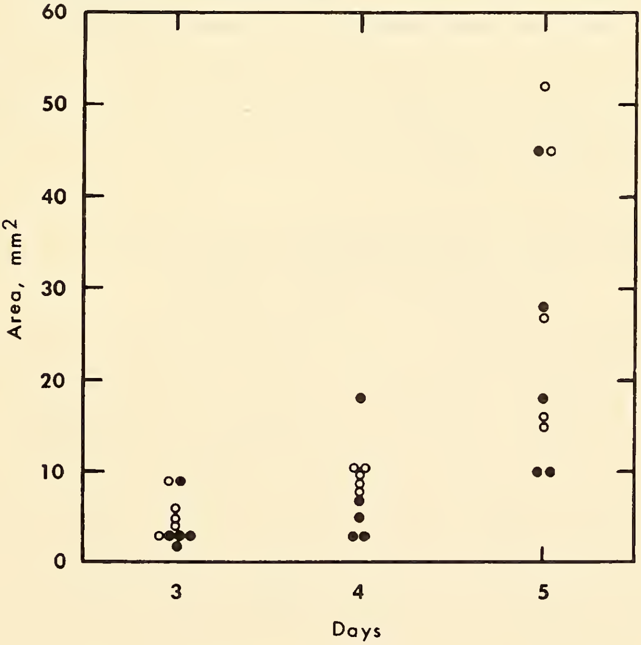


Fig. 21. The effect of moisture upon the enlargement of lesions on corn seedlings 3, 4, and 5 days after inoculation. Half the plants were exposed to the dry air (O), and half were enclosed in plastic bags (●). Experiment 3/17A.

The final measurement must be of the area of the lesion that is occupied by stalks. In Experiments 3/30A, 31, 31A, sections of diseased leaves were placed in moist petri dishes at 23 C in the light. The plants had been inoculated 3 or 4 days before, and the lesions were clearly visible when the sections were placed in the incubator. One day of incubation in the moist chamber caused stalks to appear over 25% of the lesion area, and 2 and 3 days of incubation caused stalks to appear over 50 to 60% of the area of the lesion.

I. Light and Susceptibility

The amount of sugar in the host influences resistance (Horsfall and Dimond, 1957). For example, *Helminthosporium vagans* attacks grass more severely when the sugar content of the hosts is low because the plants have been growing in the shade (Lukens, 1970). It was incumbent upon us, therefore, to find if shade and sun would change the susceptibility of corn to *H. maydis*. In Experiments 5/21, 28, four cups containing corn seedlings were placed in direct sunlight in the greenhouse, while four other cups containing seedlings were placed beneath so-called "90% shade cloth." The seedlings remained in this situation during 2 sunny days. At 1600 hours of the second day all plants were inoculated with a spore suspension and placed in plastic bags until the next morning, and then all plants were removed from the bags. Three days after inoculation the number of lesions on three leaves on each of two plants in each of two pots per treatment and experiment were counted. The results from the two experiments were consistent: the plants that had been in the sun rather than shade for 2 days before inoculation had 1/3 fewer lesions. This concludes the description of our laboratory experiments and allows us to go on and compose the simulator EPIMAY.

II. INTEGRATING THE FUNGAL CYCLE AND WEATHER INFLUENCES INTO EPIMAY

Composing a simulator is a trial-and-error business, first trying to compose, then getting needed pieces from the laboratory, then trying again to compose. For the benefit of the reader, however, we first put the laboratory observations in Chapter I, and now we show all the composing.

As the reader goes through the steps of EPIMAY, he will find parts that he remembers from the earlier EPIDEM (Waggoner and Horsfall, 1969). This is not surprising because both the *H. maydis* of EPIMAY and the *A. solani* of EPIDEM have stalks and spores, both germinate and cause lesions. If he remembers EPIDEM, he will, however, find differences because the two pathogens respond differently to weather. EPIMAY also includes an improvement, the subprogram GRATE; it accepts curves or data from the laboratory and causes EPIMAY to integrate or interpolate along these curves. Thus the employment of laboratory observations is easier in EPIMAY. The reader will also be treated—or subjected—to flow charts in our attempt to illuminate EPIMAY.

Since the reader is bound to be boggled by the hard work of analyzing the full life of *H. maydis* and relating it to the weather, he deserves some assurance of where he will come out. We can promise him that EPIMAY will run safely from lesion to stalk to spore and back to lesion, that she behaves in all her parts like *H. maydis* inoculated upon a moist leaf in the laboratory, and that she mimics the rapid 1970 march of blight up the Mississippi Valley while it hesitated on the Georgia-Florida boundary. This enticement, we hope, will get him through the head-scratching that now begins.

A. Reading the Weather Reports

The Fortran program, called EPIMAY, is printed in the Appendix. About two pages are devoted to digesting the weather reports. Most of this is lifted shamelessly from EPIDEM because both need to know the weather.

At statement 101 a title for the weather, i.e. WXTIT, is read. If the title does not say to repeat or end, the reading of the weather begins. The same card that contains the title also contains the parameter IBGN, which must be mentioned before we go on. EPIMAY has been set in her assignment of rain to days and calculation of leaf area per land area (LAI) for a May 1 beginning in the southern states where *H. maydis* came from. To start calculation IBGN days later, but with the same course of LAI, one simply punches IBGN into the last two columns of the title card; to start on May 11, for example, make IBGN equal to 10.

Since EPIMAY will proceed by steps of 3 hours, the temperature, relative humidity, wind, sunniness, and wetness are read for each 3 hours, beginning May 1 or May 1 plus IBGN days. A sunny period has less than half sky cover in daylight, and a wet period has wet leaves. This reading of weather continues for 125 days on 125 cards or until a Z is encountered in the first column of a card. At present the humidity has not been used.

Since rain will only occasionally fall, its occurrence is efficiently learned by reading cards that show only those rainy occasions or storms, not all days. The hours of beginning and ending and the inches of rain per storm are convested into inches/hour, which are assigned to the correct 3-hour periods. Rain cards are read until a blank card is encountered. The assignment of days to months by the Fortran is for cards beginning May 1. Starting June 1 requires modifications after statement 73 that can be copied from EPIDEM; this change requires a redefinition of IBGN as "days after June 1" and shifts the curve for LAI.

Sometimes one wants to know the course of disease in idealized weather. Thus, EPIMAY next includes the provision of expanding a single day into a week of synthetic climate. This ocurs in loop 587, which begins with the statement "DO 587 I=1, IEND" and ends with "587 CONTINUE." A loop begins with a command like "DO 587 I=1, IEND" and ends with a statement bearing the number of the loop, e.g. "587 CONTINUE." The loop causes everything between the "DO" and the "CONTINUE" to be repeated, here the number of days or IEND times.

Since saying leaves were dry when it was raining would be nonsense, loop 16 guarantees that when rain falls faster than .01 inch/hour the leaves will be called wet.

Finally, a summary of the weather is prepared for each day. It shows leaf wetness and rainfall in thousands inch/hour for all eight periods, nighttime humidities greater than 83%, and the number of Berger's (1970) Blight Favorable Hours, sunny periods and the mean daily temperature, relative humidity, and wind. A seasonal summary is also prepared.

The weather observations from Georgia and Tennessee that we shall use need explanation. Although southern corn leaf blight probably affected the price of food in Connecticut in 1970, a test of EPIMAY was best made by events in two southern states. A map of blight for June 18 shows that the disease had spread as far north as western Tennessee in the Mississippi Valley, but a map for July 15 shows that the disease had not yet covered Georgia (Moore, 1970). Thus a worthwhile test of EPIMAY was whether she would show the invasion of a more northern region, western Tennessee, before a more southern region, central Georgia.

At experiment stations in Jackson, Tenn. and Experiment, Ga., J. W. Measells and F. L. Crosby of the National Weather Service had taken those rare but critical observations: leaf wetness or dew. Measells rated dew in five classes, and these were converted into statements of dew at the following 3-hour periods at Jackson, Tenn.

Class	Hours of periods wet
None	None
Light	01, 04, 07
Medium	22, 01, 04, 07
Heavy and very heavy	22, 01, 04, 07, 10

At Experiment, Ga., Crosby observed dew continually with a Wong sensor. Where dew observations were missing—notably during May, 1971, at Experiment—we estimated it from the nearby weather and from the climatic behavior of dew at the station.

Conventional weather observations for airports at Jackson, Tenn., and for Atlanta, Ga., were provided as punched cards by G. L. Barger of the Environmental Data Service.

B. Fungal Character

The effect of the weather, which has now been read by EPIMAY, will depend, of course, upon the responsiveness of the pathogen. The responses are, so far as possible, taken from the experiments of the preceding Chapter. Many of the responses are in the form of "courses," e.g. the change in percentage germination or the change in the number of stalks per mm^2 with passing time. These courses are incorporated in the subroutine GRATE as values of some response Y at different values of times X. These curves will be discussed in the following pages as we reach each by following the flow charts from stalks to lesions.

Some of the fungal characters, however, can be represented by single numbers or parameters rather than a curve. For example, the wind stress

UCON that removes half the spores is a single number. If the reader looks at the Fortran, he will find these parameters in a "namelist" called FUNGUS. The code words in the list will be defined more thoroughly later, but the nature of these parameters that help define the fungal character or response can be grasped from the following list:

CL	Three fractions that represent the relative susceptibility of the host under three degrees of sunshine.
CSTK	Cold temperature that stops stalk formation, C.
HSTK	Hot temperature that stops stalk formation, C.
F	Fraction of dry spores that survives a 3-hour period.
IBEAT	Rate of rain that destroys half the stalks, inches/hr.
ICBT	Number of days from infection or penetration to appearance of lesion.
RM	Inches of rain/hour per leaf area index (LAI) that remove half the spores from stalks.
RP	Fraction of spores washed from stalks that are caught each period when 0.01 inch rain falls per hour.
UCON	Wind stress that removes half the spores (miles/hour)^2.
UCON2	Incorporates the effects of field size, maximum leaf area index (LAI) and loss of spores from the field upon the catching of air-borne spores on leaves. Dimensions of (miles/hour)$^{-UPOW}$.
UPOW	Incorporates the effect of wind speed upon the catching of air-borne spores.
WASP	Infective fraction of spores that are washed and caught.

EPIMAY learns these fungal characters on page 71 of the Fortran. At statement 107 a title for the fungal character is read. Shortly afterwards the list FUNGUS is read. The stage is now set for calculation.

C. The First Day

The repetitive nature of the calculations in EPIMAY provides a demonstration of the efficiency of Fortran. That is, the same factors of weather and fungal response must be considered each 3 hours of every day. We, however, need only write the instructions for one day within loop 99 and enclose the instructions for one 3-hour period within the loop 98 that is nested within the daily loop 99. Then EPIMAY carries on to IEND days or the end of the season.

To start, however, some accounts must be set at zero, and the simulator must be told the initial conditions of the fungus and the recent history of the weather. Thus after loop 99 is begun with the command "DO 99 I=1, IEND," the Fortran asks if "I," the day number, is 1; if it is 1, several accounts are set at zero.

The initial conditions are in the namelist called STARTS. EPIMAY gets the initial state of the fungus from only two parameters: the number of disease lesions (DLSN1) and the number of dry spores caught on the leaves (CATCH) on the first day. DLSN1 and CATCH are in the namelist

STARTS. Also in STARTS are some history: whether or not the past 16 periods were wet or dry (WP) and whether the two midday periods of the preceding day were both (IC = 1), one (IC = 2) or neither sunny (IC = 3). In other words if IC is 1 there were very few clouds, if IC is 2 there were more clouds and if IC is 3 there were many clouds during the preceding day. The list STARTS also includes a couple of variables that tell EPIMAY how to run: if DETAIL is true, details of calculation will be printed frequently, and if EXPO is true, the simulated disease will increase exponentially as if the supply of susceptible leaves were unlimited. EXPO and the related PROB will be explained fully later; for now, EXPO is true and PROB will remain at 1.

Statement 20 is reached at the beginning of every day. The number of infections NFECT in the day must be set at zero. Also the leaf area index ELAI or LAI must be calculated from the age of the crop or day number I. LAI is, of course, the foliage area per land area and ranges from about 1 at the beginning of calculation to 3 to 5 at the height of the season. In the earlier EPIDEM, the LAI followed the parabolic curve of Fig. 22, rising from about 1 on day 1 to 3 on day 80 and then declining. The rule for LAI shown in the Fortran will be discussed fully in section IVA. The parabolic rule of Fig. 22 and borrowed from EPIDEM has been removed from the Fortran in the Appendix, but it was used in the calculations of

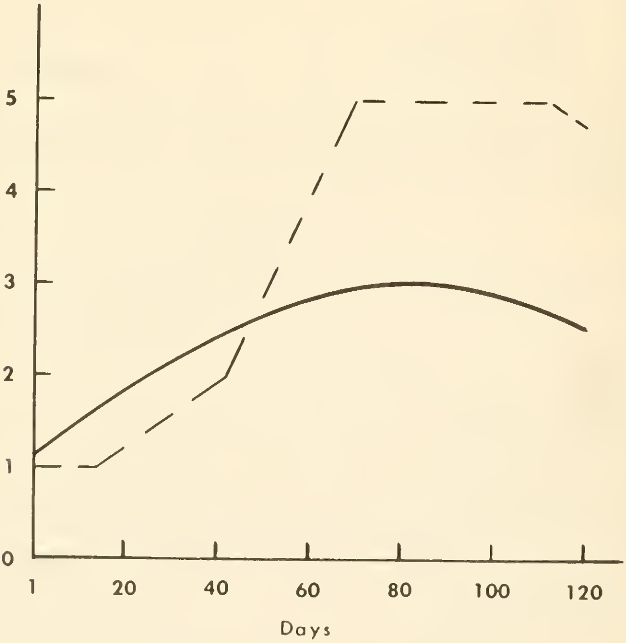


Fig. 22. The parabolic course of LAI is taken from EPIDEM and mimics potato foliage, while the angular course resembles the leaves of 20 thousand corn plants/acre (Allison, 1969; Williams et al., 1969).

the present and next chapters. The LAI calculated by either rule will be reasonable if the first day of calculation is May 1 plus IBGN for southern stations or June 1 plus IBGN for northern ones.

D. An Overview

The weather, fungal character FUNGUS, and initial conditions STARTS have been got rather easily. Now, however, we must dive into the biologic complexities. Lest we become hopelessly tangled in them, a look ahead is necessary to find some landmarks to steer by.

A flow diagram, Fig. 1, aids understanding of both the disease and the Fortran program. In one sense, the life cycle of *H. maydis* seems a complete circle from lesion to stalk to spore and back to lesion and would seem to make a circle upon a flow chart. But in another sense, the circle is broken because at some point one lesion becomes many stalks. At another point an individual spore is detached from its parent stalk and takes on a new identity. Thus, the life cycle of *H. maydis* becomes two arcs connected by dotted lines rather than a single circle (Fig. 1).

Let us begin in the upper corner of Fig. 1. The boxes or rectangles in the Figure are accounts, e.g. the number of stalks on hand. The material stuff of the fungus flows from box to box, i.e. from account to account, through solid lines, but intangible information or influence flows through dotted lines. The number of freshly formed or green stalks in the GSTK account depends upon the number of disease lesions in the DLSN account as shown by the dotted line; but a lesion is not a stalk, and the line is merely dotted, implying that it is information and not the material of stalks that is transmitted.

The freshly formed green stalks in the GSTK account may be transferred bodily along a solid line to the dry stalk or DSTK account by merely drying. Alternatively, either a GSTK or a DSTK may bear a spore, transferring the stalk into the fertile stalk or FSTK account. Then, when the fertile stalks are denuded by removal of their spores, they become dry stalks and may form another spore. So much for stalks.

Whenever a stalk enters the fertile stalk or FSTK account a spore appears in the SPOR account. Thus the dotted lines of influence connect the routes into FSTK to the SPOR account. Also, when spores are carried away, the DSTK account is increased, and dotted lines extend from the SPOR exits to the route back to DSTK. Thus a stalk is not a spore, but the two processes are connected.

Spores are carried from the stalks via wind or rain, and they pass through the AERIAL or AQUA account. When they land on new host tissue, they enter the CATCH account. Air-borne spores, being dry, may remain inertly in the CATCH account, but the rain-borne spores go immediately to the wet catch or WCATCH account. The air-borne spores also enter the WCATCH account as soon as they are wetted.

The spores in the WCATCH account gradually germinate and enter the GERM account, or if they dry, they are killed. If the leaves continue wet, the germinated spores penetrate the leaves and enter the incubation or

NCBT account. After a period of invisibility, a unit in NCBT becomes a disease lesion in the DLSN account and can in time become a multitude of stalks to appear in the GSTK account, thus completing a fungal generation. The route from SPOR to DLSN is a solid line, showing that the mycelium in the lesion DLSN is but an enlargement of a single spore from the SPOR account. This overview of the life of *H. maydis* and of its mimic EPIMAY prepares us for the detailed examination of the flow chart and Fortran, which follows.

E. Stalks Are Formed

The portion of Fig. 1 that concerns stalks is amplified in Fig. 23. This flow chart generally follows the conventions of Forrester (1968). A valve (⧖) is a rate; e.g. the STALK valve shows an addition of so many stalks per period to GSTK. A valve that looks like a butterfly (▷◁) is a rate that equals another rate; e.g. the lower exit from FSTK has the same rate as another valve that will be described on another chart. The boxes are accounts that have a level like a bank account; e.g. GSTK is the number of fresh or green stalks in our universe of a field. The small circles, e.g. IGLS are variable parameters calculated on the way to learning what the rates are. Large circles, e.g. WET, are weather factors. Constant parameters are written next to a line, e.g. IBEAT. Things, as green stalks GSTK that bring material from outside the diagram come from clouds, and things as beaten stalks that are lost depart to clouds in the diagram.

As we examine Fig. 23, reference will also be made to the Fortran program. Stalk formation begins soon after the statement "DO 98 J = 1, 8," which initiates loop 98. Loop 98 is repeated each 3 hours until eight loops are completed to make a full day of 24 hours, completing loop 99. For each 3-hour period there is a temperature, a wind speed, and a rate of rainfall. There is also a statement that leaves are wet or dry. If it is the first or second (0100 or 0400 hours) or the last (2200 hours) period, it is dark, and there is a statement that LIT is false, a hard way of saying that it is dark at night. These weather or environmental factors appear in circles TEMP, RAIN, WET, and LIT upon Fig. 23. WIND will appear on a later diagram.

The stage is now set for calculation. Stalk formation is the first step. Since the lesions will be too small for stalk formation on the first day, stalk calculation is passed over on the first day with the command "IF (I.EQ. 1) GO TO 31."

In the flow diagram a valve named STALK regulates the flow into the GSTK account, which flow is the growth of stalks upon the lesions. STALK is controlled by the parameter IGLS, among other things. The index of stalk formation, IGLS, is controlled by WET; this is so because in Experiment 3/17A stalks did not form on lesions unless the diseased leaf was enclosed in a plastic bag to keep the leaf moist. This observation is not only embodied in the flow chart but also in the Fortran close to statement 25 where we say "IF (.NOT.W(I,J)) GO TO 30." This means that if the

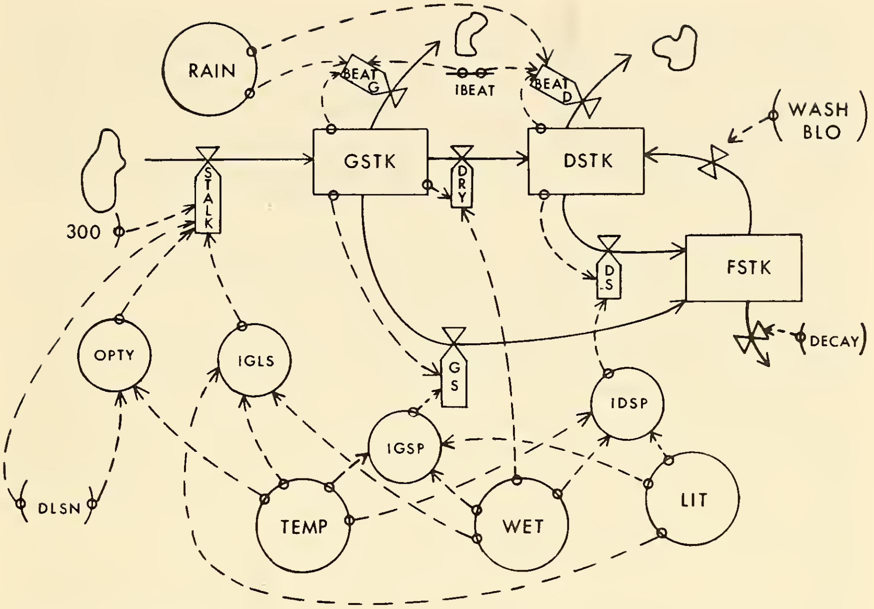


Fig. 23. The formation of stalks and their sporulation under the influence of temperature, wetness, light and rain.

leaf isn't wet, at period J on day I, calculation should pass over the formation of GSTK, go to statement 30, and there transform all GSTK into DSTK. This is quickly done but requires some explanation, which will be provided after we see how the GSTK were formed when the leaves were wet, i.e. when W(I,J) was true for day I and period J.

In his examination of the Fortran, the reader will already have discovered that there is more than one GSTK account. In fact, there are 16 from GSTK (1) to GSTK (16). Other accounts and even indices also appear in multpiles. This multiplication of accounts is necessary because not all GSTK are alike: some were formed 1 period or 3 hours ago and some 3 times 16 or 48 hours ago.

If leaves are wet, new stalks can be formed in the present period. Thus we must make room for them in GSTK (1). So that those in GSTK (1) will be those formed in the present period, while those in GSTK (2) were formed 3 hours ago, the accounts must be moved into the past. Loop 29 moves GSTK (1) to GSTK (2), and so forth. While we are at it, some other accounts are also moved.

Unfavorable temperatures can prevent stalk formation even when leaves are wet. When the temperature is cooler than CSTK or hotter than HSTK, therefore, calculation of stalk growth is passed over with the command "IF (TNOW. LE. CSTK. OR. TNOW. GE. HSTK) GO TO 31."

The first task in calculating STALK is identifying the appropriate curve for the increase of IGLS and hence stalks per mm^2 of lesion. These curves are in Fig. 6, and they show the course of relative stalk numbers per area for fully three days or three times eight periods of 3 hours. The courses range from no stalk formation at 35 C in the light or practically no stalk formation at 14 C in the light to fairly rapid formation at 30 C in the dark and on to the most rapid formation at 30 C in the light. These ten curves are 1 to 10 in subprogram GRATE. Thus six early statements in STALK are used to select the curve L according to temperature and light (here L is a subscript, not light).

The next step is searching over past days; these past days are identified by a subscript K. On day 5 the search would be from K equal 4 to K equal 1. Two things are examined for each day past: IGLS and OPTY, two parameters that affect the STALK valve in flow diagram Fig. 23.

IGLS(K) is the index of relative stalks per area of DLSN(K) that appeared on day K. Since IGLS grows regularly in size from 0 to 1 in Fig 6, finding say, IGLS(2) is 1 means the lesions that appeared on day 2 and day 1, too, are fully stalked. OPTY(K) is the area or opportunity for stalks on the lesions appearing on day K; finding, say, OPTY(2) is zero means there is no room for stalks from DLSN(2).

Now suppose OPTY(3) is 2 mm^2 and IGLS(3) is 0.5, meaning that the lesions appearing on day 3 are now 2 mm^2 in size and have 0.5 their full complement of stalks. If the temperature is 30 C and it is daytime then the subprogram GRATE will find a 3-hour increment of IGLS of 0.1 on curve 7 for an attained IGLS of 0.5. Curve 7 is 30 L in Fig. 6. The three-hour increment on curve 7 will increase IGLS(3) from 0.5 to 0.6. It will also cause the account for presently formed stalks, GSTK(1), to be increased by the product of the increment OPTY(3) 300, and DLNS(3). The 300 is the maximum density of stalks formed per mm^2 of lesion in Experiments 4/13, 20. If 100 lesions had appeared on day 3, the increment in GSTK(1) would be:

$$(0.6\text{-}0.5) * \frac{2\ \text{mm}^2}{\text{lesion}} * \frac{300\ \text{stalks}}{\text{mm}^2} * 100\ \text{lesions.}$$

This process is continued for all past days that have IGLS less than 1.0 and that have any DLSN. Note that this simple method of calculation overlooks the stalks that could be grown on the *increase* in OPTY(K) between an IGLS of zero and the size of IGLS(K) reached by day 1. Finally, we go to statement 38 where a census may be printed.

The reader may be struck by our using the attained level of IGLS, rather than a time, to look up the new IGLS and thus its increment. First, let us examine what would happen if we had used a time, say the hours of wetness. Then IGLS and stalk growth would have proceeded rapidly along the left end of the curves of Fig. 6 at the beginning of a wet period and slowly along the right end of the curves after a long wet period. This would happen whether the lesions were bare or nearly covered by stalks, a most unrealistic process. Instead the subprogram STALK picks a curve from Fig. 6 according to temperature and light, locates the current condition of the lesion (that is, its IGLS) on the chosen curve, and then moves up the curve one period.

Now let us see how these computations are depicted in Fig. 23. The flow of stalks to GSTK is regulated by the valve STALK. Its operation is affected by the maximum density 300, by the area OPTY, and by the index IGLS. IGLS, in turn, is affected by LIT, TEMP and WET. That is how the GSTK account is filled. How is it emptied?

A simple exit from the GSTK account is opened when leaves dry. Then the valve DRY between GSTK and DSTK opens, admitting GSTK to the DSTK account. The distinction between the contents of these two accounts or boxes in that GSTK have never been dry while DSTK have. The distinction was necessary because drying causes stalks to produce spores more slowly. Thus Fig. 8 shows that fresh or green stalks become fully laden with spores in 6 hours, while Fig. 9 shows that stalks once dried sporulated more slowly. Hence in loop 44 the GSTK are all converted to DSTK when leaves become dry.

Another simple exit from GSTK is through valve BEAT G, the beating by RAIN. After a quarter-inch or 6 mm of artificial rain in Experiments 3/17 B, 6/3 only three-quarters of the stalks were capable of producing spores. This experience is summarized in the equation:

$$\text{BEATER} = \text{IBEAT} / (\text{IBEAT} + \text{RAIN}).$$
$$3/4 = 3/4 / (3/4 + 1/4).$$

In other words, IBEAT is the rate of rain that destroys half the stalks. Thus in loop 34, GSTK and DSTK, too, are reduced if rain falls.

F. Spores Appear

The third exit from GSTK leads to the fertile stalk account FSTK via the valve GS. This is the sporulation of green stalks, which makes them into fertile stalks. First in the Fortran wetness is investigated and sporulation curves L and K are identified according to light and temperature. Then, beginning at Fortran statement 32, we calculate the GS to subtract from GSTK and add to FSTK. Since Fig. 8 shows few spores after 3 hours (one period) no calculation is made for M equal 1 or the current wet period. If, on the other hand, the first past period is wet, i.e. WP(1) is true, and some GSTK(3) appeared two periods ago and were available for sporulation during the past period, the index of sporulation IGSP (3) is increased to the maximum allowed by the current temperature, Table 1. This is justified because maximum sporulation is reached in 6 hours on stalks that are always moist, Fig. 8. For example at 18 C in the light 88% of the GSTK bear spores in 6 hours. These values or maxima are incorporated in curves 12 and 13 of the subroutine GRATE, and in the main program. GRATE(5, K, DUM, TNOW) commands the computer to interpolate the sporulation index on the curve K for dark or light and the TNOW, the temperature now. The "5" orders interpolation, K picks the curve, and DUM is a dummy. The new IGSP has thus been calculated from temperature TEMP, wetness WET, and light LIT, as the flow chart, Fig. 23, shows. The increment in IGSP is next used, together with the account GSTK, to calculate the rate GS. Since GSTK is depleted after each cycle, while the IGLS curve concerns percentages of an original, undepleted stock of stalks, the increment is divided by the proportion (1 — TEMP) of stalks remaining (TEMP is temporary, not temperature, here). We have now examined all the exits from the account GSTK and turn to DSTK, which also has an exit to FSTK or the account for spore laden stalks.

Now, what of sporulation on the DSTK, which were found when the GSTK were dried? The essential difference between GSTK and DSTK is the slower sporulation of the DSTK. These slower rates depend upon temperature, wetness and light as the flow chart, Fig. 23, shows. These slower courses of sporulation are depicted in Fig. 10. The increase of IDSP is calculated from these same curves incorporated in GRATE. Within loop 45 a new IDSP(M+1) is calculated for each past DSTK(M+1) account when the leaves were wet and DSTK(M+1) was not zero. When M is 2 in the loop, we consider IDSP(3) and DSTK(3) formed two periods before and available for sporulation one period or 3 hours before. The wetness 3 hours before is described by WP(1). The increment in IDSP(3) is calculated for the period 3 to 6 hours past on curve 30 to 37 of IDSP in GRATE. Finally the rate DS is calculated.

The GS and DS are subtracted from the accounts GSTK and DSTK. According to the flow chart, Fig. 24, the DS and GS should be added to the fertile stalks FSTK. So they will, but a few bookkeeping devices are introduced into the Fortran. First, since FSTK equals SPOR, SPOR is used for both FSTK and SPOR in the Fortran. Second, since the new spores should not disperse in the same period that they form, the new spores are kept in a special account SPORI that will be added to the total account SPOR after statement 60 when dispersal has already been calculated.

Since *H. turcicum* spores decay to a small percent of viability after 6 months (Robert, 1964), both SPOR and CATCH on new sites are decayed to a fraction F each 3 hours. Although we have employed a survival or F of fully 0.993, this valve will decrease viability to less than one in ten thousand after 6 months. The calculation of this decay of SPOR and CATCH follows statement 39. Since there is a loss from FSTK equal to this loss from SPOR, a butterfly valve DECAY controls the loss from FSTK in Fig. 23.

The life of the spore from SPOR to visible lesion DLSN is depicted in flow chart Fig. 24. Spores equal to DS and GS enter SPOR, and decay subtracts spores. The most important process, however, is the dissemination of the spores on rain and wind via the AQUA and AERIAL accounts.

G. Spores Are Washed Off Stalks by Rain and Caught by Leaves

The departure by washing is calculated next in the Fortran program. On the flow diagram the rate between SPOR and AQUA depends upon the number in SPOR. It also depends upon the parameter WASH. WASH in turn depends upon the rate of rainfall, the leaf area LAI, and a parameter RM.

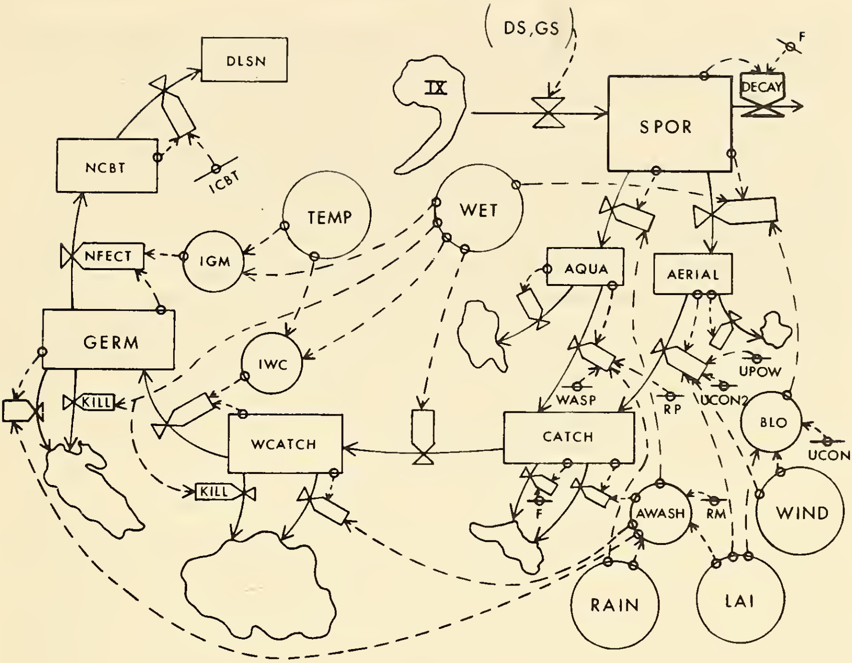


Fig. 24. The formation of lesions from spores under the influence of rain, wind, temperature, wetness and leaf area index.

In the earlier EPIDEM the great uncertainties were in the dissemination process. While the effect of environment upon the progress of, say, germination was not only identifiable but also measured in the laboratory, the effect of wind or rain upon the spread of spores was not easily measured although the parameters had an identifiable nature. Things are the same in EPIMAY.

Since the parameters have an identifiable nature, we can at least use common sense to estimate them. RM is the inches of rain per hour that remove half the spores. It is reasonable to measure the rain per unit of leaf area rather than per ground area. Hence the fraction of the spores washd away AWASH is calculated as

$$\mathrm{AWASH} = \frac{\mathrm{RAIN/LAI}}{\mathrm{RM} + \mathrm{RAIN/LAI}}$$

If we calculate

$$\mathrm{RL} = \mathrm{RM} * \mathrm{LAI},$$

then

$$\mathrm{AWASH} = \mathrm{RAIN}/(\mathrm{RL} + \mathrm{RAIN})$$

We now assume that RM is 0.04 as we assumed earlier in EPIDEM; then a quarter-inch of rain per hour on one leaf area removes 86% of the spores. This 86% is responsible because in Experiments 3/17B, 6/3, a drop of water removed all the spores that it struck. During a rainy period the AQUA account is increased to the product of SPOR by AWASH, while the residue of SPOR by WASH stays behind (WASH is 1.-AWASH).

The AQUA account is immediately emptied via two routes. The more important route passes to the account CATCH, which is the number of spores at new infection sites. The number traveling this route is, of course, proportional to the number in AQUA. The flow diagram shows RAIN, RP and WASP also influence the valve; what are these doing here?

Dissemination is the uncertain part of EPIMAY, but we can identify some reasonable processes. The first process is the dilution or greater washing of spores to the ground by greater rainfall. If one unit of rain leaves only 0.9 of the AQUA account to be caught, then two units should leave $(0.9)^2$ and three $(0.9)^3$. We have arbitrarily used one-hundredth inch of rain per hour or RPOW as our rainfall unit, substituted RP for 0.9 in the example, and written into the Fortran.

$$\mathrm{RP}^{100\ \mathrm{RAIN}} = \mathrm{RP}^{\mathrm{RPOW}}$$

It also seems reasonable that only a fraction of the spores that are not washed to the ground will be effective in reaching a new host. Since we shall assume that this is a constant fraction WASP, we incorporate in it both the concept of "chance of reaching a host" and also the concept of "infection efficiency." The latter is the ratio of lesions produced to spores applied under optimum conditions, and Experiments 7/15, 20, showed it was 0.2. Thus WASP must be less than 0.2, and we chose the 0.05 for WASP that behaved reasonably well for *Alternaria* in the simulator EPIDEM.

Combining the number of spores in the AQUA account and the conventions of RP and WASP, we calculate the increase in CATCH:

$$\mathrm{AQUA} * \mathrm{WASP} * \mathrm{RP}^{\mathrm{RPOW}}$$

Rains of a tenth- or quarter-inch per hour would remove 71 or 86% of the SPOR and then catch 2 or 0.3% of the spores awash. In the Fortran, the above expression is multiplied by PROB, but PROB is still 1 and has no effect yet.

Thus lines of information go to the valve below AQUA and above CATCH from WASP, AQUA, RAIN, and RP. The remaining spores in AQUA are lost into a sink. In nature this would mean that they had fallen on stony ground. Since the residue is completely lost, the valve leading to a sink from AQUA is simply controlled by the number left in AQUA.

Related events happen at the same time spores are moving from SPOR through AQUA to CATCH. Some of the spores are lost from an account called CATCH, others are washed from the account WCATCH, and germinated spores are also washed away.

Finally, the removal of spores from stalks, i.e. from the account SPOR, means that the stalks are denuded and may again bear spores. They will bear them slowly as the stalks in the DSTK account. This is evident in Table 3. Therefore, if the reader will look back at flow diagram Fig. 23

concerning the formation of stalks, he will find a butterfly valve admitting stalks from the FSTK account to the DSTK account. Whenever spores are washed from the SPOR account, an equal number of stalks is transformed from the FSTK to the DSTK account.

H. Spores Are Blown by Wind and Caught by Leaves

We are now ready to examine the travel from the SPOR to CATCH account on the wind and via AERIAL. Since *Helminthosporium* spores rarely appear in the air in wet weather (Meredith, 1966), statement 59 causes EPIMAY to pass over this section in wet or windless weather. On the other hand, dry *Helminthosporium* spores were easily blown from stalks in Experiments 3/17, 4/14.

The proportionality between wind speed and air-borne *Alternaria* spores (Rotem, 1964) led us to relate the take-off of spores in EPIDEM to the wind stress, i.e. the square of the wind speed. In corn the wind decreases from the full reference wind speed across the first leaf area index to a half at the second and to a quarter at the third leaf area index (Brown and Covey, 1966). This means that the stress on the spores falls from the full *square* of the reference wind on the first leaf area to a quarter on the second and to only a sixteenth on the third leaf area. If one averages these three stresses over the three leaf areas per land area, he gets .44. If the .44 is multiplied by the square of the wind speed at reference level, the mean stress on the spores through a leaf area of 3 is obtained. Curve 14 in GRATE embodies this relation between mean stress through the canopy and the leaf area index. Hence the mean stress TAU is got by multiplying the square of the reference wind speed by the function GRATE with an argument of 5 for interpolation, an argument of 14 for curve 14, a dummy and finally the leaf area index ELAI. We are now almost ready to calculate the parameter BLO, only needing to explain that the parameter UCON is the stress that removes half the spores. The parameter BLO is now calculated as the mean stress divided by the sum of the mean stress and UCON. A 5-mile-per-hour wind over an ELAI of 3 would remove about 5% of the spores in a 3-hour period and put them in the AERIAL account.

In the flow diagram, the valve controlling the flow from the SPOR to AERIAL is controlled by three pieces of information. First, if the leaves are wet, the spores cannot be blown. The second and third pieces of information are the account SPOR and the parameter BLO. If the reader now looks at the Fortran program near statement 60, he will see that the SPOR account is decreased according to its size and BLO. Thus AERIAL is SPOR times BLO. The stalks that have been denuded by the wind are now available for a new crop of spores, and hence the account DSTK is increased by the same product of SPOR and BLO; these denuded stalks are placed in DSTK rather than GSTK because Table 3 shows that the denuded stalks re-sporulate at the slow rate of DSTK.

The next problem is catching these spores that are briefly in the AERIAL account. We have employed several parameters that were introduced in the earlier EPIDEM. First it is reasonable that the proportion caught will increase with the abundance of foliage or LAI. It is also reasonable that the greater turbulence accompanying a faster wind speed U will carry more spores beyond the region that concerns us; this is accomplished by dividing by U raised to a fractional power UPOW. Finally, the proportion UCON2 caught in a field with an LAI of 1 and in a 1-mile-per-hour wind must be established. Like the fraction WASP in the preceding section, UCON2 must be less than the observed infection efficiency of 0.2. Thus, the fraction of AERIAL caught will be $ELAI/(WIND^{UPOW}) * UCON2$. This latter expression is multiplied by PROB in the Fortran, but PROB is 1 for now and has no effect. In the flow diagram, Fig. 24, the valve regulating the flow from AERIAL to CATCH accounts is controlled by LAI, the WIND, the parameters UPOW and UCON2, and finally the number of spores in the AERIAL account. Since other spores in the AERIAL account blow beyond our consideration, the valve leading from the AERIAL account to a sink is controlled simply by the residual AERIAL spores. When UCON2 is .02, LAI is 3, UPOW is 0.5 and the wind is 5 miles per hour, the above rule catches about 3% of AERIAL. In other words, 97% of the air-borne AERIAL spores follow the lower right route of Fig. 24 to oblivion, while 3% follow the lower left route to CATCH.

A summary explaining the spreading of spores is now in order. This spreading has taken us from instruction 39 to 60 in the Fortran program. On the flow diagram it has taken us from the account SPOR to CATCH. We have spoken of a slow deterioration of the spores governed by a parameter F, of the movement of spores into the AQUA or AERIAL account in the rain or wind, of the catching of a proportion of those spores on new infection sites, and of the loss of the remainder of the spores on stony ground or on the wind. The renovation of stalks into the dry stalk DSTK account has also been mentioned. The washing of the SPOR account is, of course, accompanied by a washing of spores from the CATCH, WCATCH, and GERM accounts.

I. Spores Germinate

Despite earnest attempts in Experiments 3/9A, 12, we never succeeded in germinating spores in the absence of water droplets. Thus before they can germinate, CATCH spores must be wetted, i.e. moved to WCATCH. If the spores have arrived at CATCH on the wind, they will be dry and can remain in the dry CATCH for a long time. Only a few will leave via the slow deterioration regulated by F. If, however, they have arrived in CATCH in rain, they will immediately pass into WCATCH. Alternatively, if they have arrived on the wind and have accumulated in the CATCH account for some time, they will move to WCATCH only when wetted by rain or dew. Thus, the valve regulating the flow from CATCH to WCATCH is controlled by information on leaf wetness. Since the spores that have just arrived in WCATCH must not be confused with those that arrived earlier, we first move the older spores by means of loop 61 in the Fortran program. We also move their index IWC. Finally, CATCH is placed in WCATCH(1) and CATCH is left empty.

Now that spores have reached the moisture of WCATCH, the simplest way out on the flow diagram is through the valve KILL. In Experiments 3/9B, 11A, spores once wetted and then dried were killed. Therefore, valve KILL, which empies WCATCH, is activated by information about wetness. This depletion of the WCATCH as well as the similar killing of the GERM account occur in loop 67, but these are not very interesting outcomes.

The path from WCATCH to GERM, which is traveled as spores germinate, is more interesting. We have observed the germination of spores at a variety of temperatures, and the observations are summarized by Fig. 25 and by curves 22, 23, and 24 in the subprogram GRATE. (Fig. 25 was incorporated into the simulator before Experiment 6/22, and we have continued to use Fig. 25 rather than Fig. 13 in EPIMAY.) If the temperature is 5 to 40 C, one of these three curves in Fig. 25 is selected in the Fortran program. These curves permit the calculation of the index IWC, which Fig. 24 shows controlling the path from WCATCH to GERM. Loop 62 recalls the WCATCH accounts, increasing the IWC index for each of the accounts wetted in a preceding or the present period: WCATCH(1) was wetted in this period, WCATCH(2) in the preceding one, WCATCH(3) in the period before that, and so forth. Beginning loop 62, we know that leaves are now wet; and, therefore, when M is equal to 1, we go directly to statement 64. IWC must be less than 1 or no further increase is possible. If IWC is less than 1, statement 64 is passed. If there are no spores in WCATCH(1), no increase in IWC is necessary, and therefore, we go to the end of loop 62. If, on the other hand, there are spores in WCATCH(1), we calculate a new IWC by adding an increment along one of the curves of Fig. 25, just as other indices have been increased. Then, as the valve between WCATCH and GERM suggests, we multiply the increment in IWC by WCATCH and add this to GERM(1), which is the number of spores that have germinated in the present period. Loop 62 is repeated for as many as 16 past periods if they have been wet and have ungerminated WCATCH. When the number of past periods continuously wet has been exhausted, we go to instruction 70 and print a census.

J. Germinated Spores Invade Leaves

The next step for EPIMAY or *H. maydis* is to infect leaves with the germinated spores. This is the route on the flow diagram Fig. 24 from GERM through the valve NFECT into NCBT, the account for incubating lesions. Figs. 17 and 18 show that penetration increased regularly with duration of wetness and according to temperature. Bearing in mind the role of germination in penetration of leaves by inoculum, we constructed Fig. 26 and the curves 27, 28, and 20 in GRATE. Thus the index IGM is increased according to the level of IGM already attained; this is accomplished in loop 71 after a curve is selected for the temperature. Spores germinated within the present period, i.e. GERM(1), can also penetrate within the present period as was shown in Experiments 3/10, 17C or Fig. 17. On the flow diagram the valve NFECT is controlled by IGM and the number of

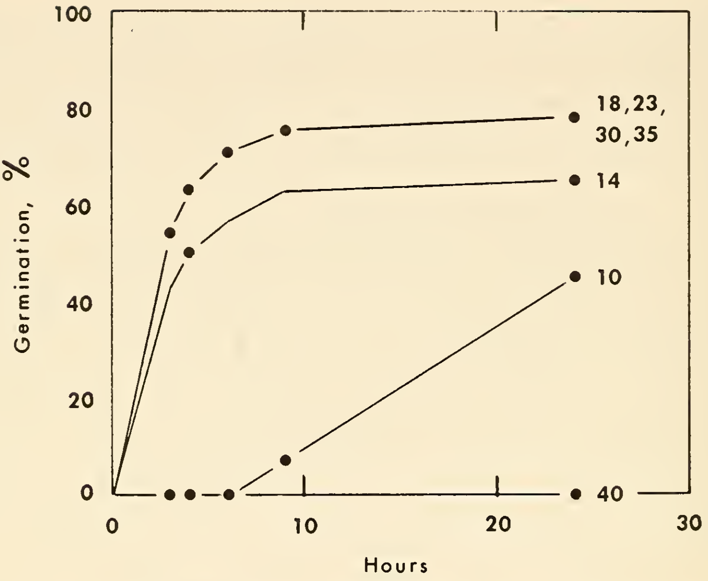


Fig. 25. The course of germination used in the simulator. Experiments 2/25, 3/3, 5, 11, 5/11.

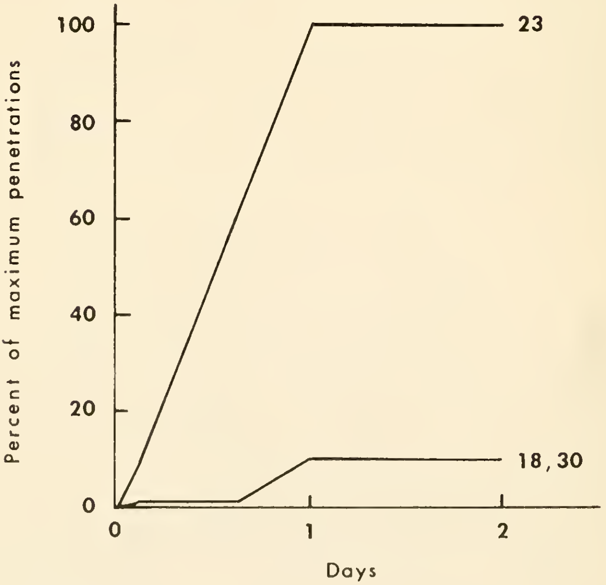


Fig. 26. The course of penetration used in the simulator. Derived from Experiments 4/5, 15, 5/3.

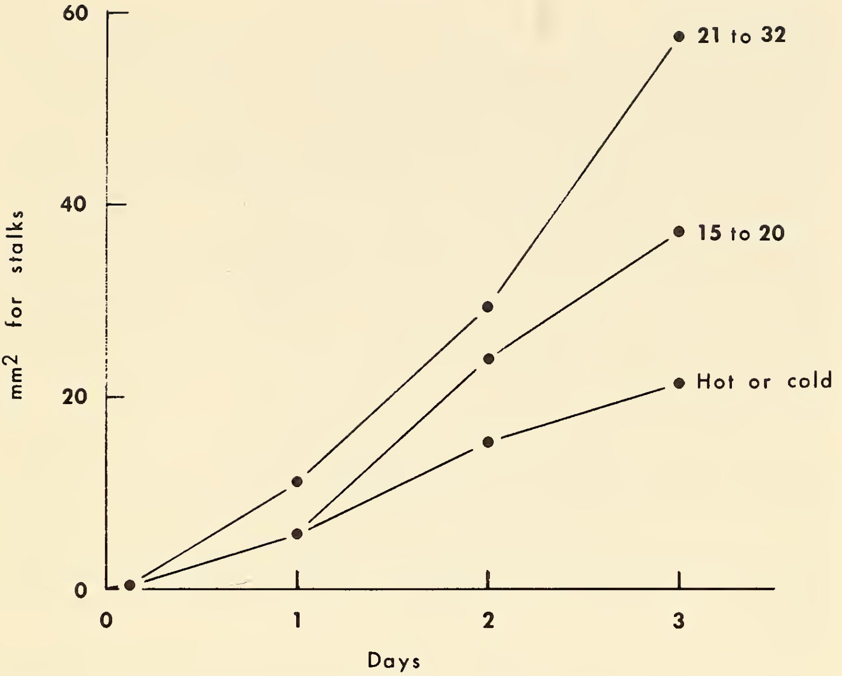


Fig. 27. The enlargement of the area of stalks on lesions as used in the simulator. Derived from Experiments 3/17A, 17D, 22, 30A, 31, 31A, 4/13, 20.

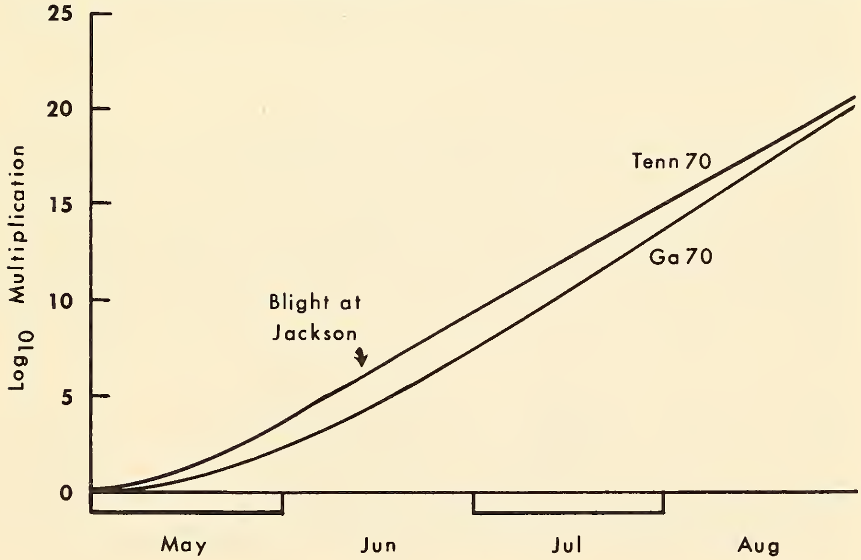


Fig. 28. The simulated epidemics in Tennessee and Georgia in 1970. The time of blight report at Jackson, Tennessee, is shown.

spores in GERM. NFECT is simply the increment in IGM times GERM times CL(IC).

CL(IC) must be explained. The susceptibility of corn increased in shade in Experiments 5/21, 28. In those experiments plants in 90% shade for two days before inoculation developed fully half again as many lesions as plants in full sun. Now CL(IC) is one of three factors chosen according to sunshine the preceding day. Attention is directed to 10 and 13 hours when the potential for insolation is greatest. If sky cover was less than six tenths, the period was called "sunny." If it was sunny at 10 and 13 hours, IC is 1; IC is 2 if one period was sunny; and IC is 3 if both periods were cloudy. In the Fortran, the IC is chosen according to cloudiness shortly after statement 98 is passed at midnight. In our first calculations, all three CL have been set at 1, allowing no effect of sun upon susceptibility, but we shall later explore the effect of cloudiness by further calculation.

The reader may wonder why the accounts GERM are not depleted during the calculation of penetration. He may already have begun to wonder when he found that the accounts WCATCH also were not depleted by germination. Depletion is not necessary because the addition to NFECT is taken as the increment in IGM rather than the attained level of IGM. For example, if IGM rises from 0.7 to 0.8 for a GERM account of 100, the addition to NFECT is 100 times the difference between 0.7 and 0.8, or 10 new infections.

In the Fortran program for the 3-hour period, there are no further calculations regarding NFECT after statement 75. Thus, the infections for the day accumulate in NFECT for fully eight periods. Then at midnight or just after statement 98 the NFECT are dumped into an NCBT account identified with the day of infection. In this way valve NFECT is passed as the flow diagram says it will be.

K. Infections Incubate

How do the incubating lesions become visible lesions DLSN? This occurs when ICBT days have passed. In our experiments, this took about 3 days. That is, in Fig. 20 the first pin pricks appear after 2 days, but the lesions were free of stalks on the third day and only a few appeared upon the fourth day. As Fig. 20 shows, the time for appearance of the first small lesions was not greatly affected by temperature. Therefore, passage from NCBT to DLSN is controlled on the flow diagram Fig. 24 solely by the number of incubating lesions and ICBT, the length of incubation. In the Fortran program this process is performed shortly after statement 98, which is passed at midnight. As an illustration, assume it is midnight on day 5. The NFECT going into incubation are called NCBT(5). The visible lesions coming out of incubation are called DLSN (I + 1) or DLSN(6). They are the infections that occurred on day (I —ICBT + 1) or day 3, and they will be DLSN(6), in the first or 0100 hour period on day 6.

L. Lesions Enlarge

When the DLSN first appear, they are too small to bear any stalks. As the hours pass, however, they grow in the manner shown in Fig. 20. A fraction of the lesion, from about a third after 1 day to two-thirds after 2 or 3 days, was occupied by stalks in Experiments 3/3A, 31, 31A. These observations and those of Fig. 20 are combined to make Fig. 27 and curves 15 to 17 in subprogram GRATE. The control of STALK formation by the lesion area, called OPTY, is depicted in flow chart Fig. 23. No line connects WET to OPTY because Fig. 21 reveals no effect of wetness upon lesion enlargement. The calculation of OPTY begins when a DLSN appears and proceeds according to the temperature; the process lies between statements 75 and 81 in the Fortran. After a curve is selected from Fig. 27 appropriate to the temperature, the OPTY(K) for past days K are accordingly increased. They are increased from their attained size by the increment observed during a 3-hour period on lesions that had attained the same size, Fig. 20.

Up to now our attention has been upon the fungus, and the host has been neglected as a mere medium that feeds the fungus and allows it to spin around the flow charts. The observer in the field, however, will have a different view; he will rarely count stalks or spores and will usually neglect the number of lesions in favor of noting the percentage of the tissue diseased. Thus we must simulate the population of fungi in the accounts of the flow charts for it is the fungi and not the lesions that multiply. Nevertheless we should translate these into the percentage of tissue diseased. This can be accomplished by defining the area of the field and employing the parameters LAI, DLSN and OPTY.

The initial number of lesions DLSN1 or spores CATCH that started the simulated epidemic was not restricted to a certain field size, say, a hectare. Thus the numbers in the accounts, e.g. DLSN(I), are the fungal population or lesions per initial infection DLSN1 or CATCH, not the population or lesions per hectare. Before we can calculate the percentage of tissue diseased, we must change this situation by relating the initial DLSN1 or CATCH and its progeny to a certain land area. Let us decide that the DLSN1 or initial CATCH was in a hectare.

The leaf area that can be diseased on a hectare is simply the 10^4 m^2 or 10^{10} mm^2 of a hectare multiplied by the leaf area index ELAI; this product is calculated at midnight, i.e. after statement 83, and called HECTAL. Since the area of diseased leaf is 3/2 of the stalk bearing area or OPTY, the diseased area in the hectare is

$$3/2 \sum_{K=1}^{I} \mathrm{OPTY(K)} * \mathrm{DLSN(K)}$$

or the area of all the lesions that have appeared between days 1 and I. This sum of products of OPTY and DLSN is calculated in loop 83 and called TEMP, the temporary variable of all work. The final step is calculating the percentage of the leaf area diseased by dividing foliage area HECTAL into lesion area TEMP.

A summary is in order. A flow of material is indicated on flow chart Fig. 24 all the way from the SPOR account to the visible lesion account DLSN. This is shown as a solid line or flow of material rather than a dotted line of information because one spore could begin at SPOR and move either through the AQUA or AERIAL account to CATCH onto WCATCH onto GERM through NCBT and become a visible disease lesion DLSN. Along the way it might have been blown by wind or washed by rain into the CATCH account, avoiding the perils of falling on stony ground or being blown from the plot. Wetting would then have moved the spore from the CATCH to the WCATCH account. Germination regulated by moisture and temperature would have moved it to GERM. Next the spore would have had to succeed through the infection process, also regulated by temperature and moisture. As long as it was in WCATCH or GERM, it was exposed to death by desiccation. Finally, it would have had to have spent 3 days in the chrysalis of incubation. Then it would appear as a lesion, grow and become a home to a crop of stalks. This completes the cycle of *H. maydis*. EPIMAY repeats the daily cycle to season's end.

The final task for EPIMAY is writing a summary. First she writes the number of new lesions DLSN(I) that appeared on each day I. Then the accumulated number of lesions is written. At last the logarithm of the initial DLSN1 is written at day 1 and the logarithm of its accumulated multiplication by each day is written. With these summaries completed, EPIMAY is also complete. Will she mimic actuality, verifying the essential accuracy of our analysis?

III. THE REALISM OF EPIMAY

Eventually we shall want to use EPIMAY to distill from a plethora of weather observations or forecasts a single index of the favorability of the environment for *H. maydis*. This will provide disease forecasts or, looking backwards, a climatology of disease. We shall also want to use EPIMAY to reason how changes, for example in speed of incubation, would alter an epidemic. Before we can safely employ her, however, the realism of EPIMAY must be established.

The realism is established by answering three questions. Are the components logical and measurable? Does the whole simulator mimic a simple course of fungal life in a constant environment? Does the simulator reproduce well known differences in epidemics of the past?

By reflecting on the pages that have gone before, the reader can answer the question, "Are the parts logical?" EPIMAY is not a single rule relating, for example, disease loss to rainfall. Neither is she a single differential equation, saying the fungus will multiply by a constant percentage each week. Instead the flow diagrams show logical steps or parts of the fungal cycle that the biologist can identify. The parts have values that can be — and generally were — measured in the laboratory or field. Thus EPIMAY has already passed the first test of realism.

Now, does the assembly of all these parts into the whole simulator mimic a simple course of fungal life in a constant environment? In these calculations and those that follow in this section, the parameters had the following values: CSTK, 11C; HSTK, 33C; F, 0.993; IBEAT, 0.75; ICBT, 3 days; RM, 0.04; RP, 0.9; UCON, 200 (miles/hour)^2; UCON2, 0.02; WASP, 0.05. The CL were all 1. The simple course of disease following the inoculation of a plant with 100 spores in a moist chamber was simulated. The temperature was constantly 70F (21C), and the leaves were constantly wet for 7 days. Wind, sun and relative humidity were irrelevant. It was light, of course, from 07 to 19 hours.

The outcome is seen in Table 4. Sixty percent of the spores germinated in the first 3 hours. Subsequently germination rose to a maximum of 80 percent as in the experiments summarized by Fig. 25. The first 3-hour period also permitted a few penetrations of the leaf; it is well that it does because a few infections are shown in Fig. 17 even when the leaves were inoculated with freshly suspended spores and then dried after only 3 hours. Infection continued to increase more or less linearly for fully 24 hours, much as in Fig. 17, where the infection attained was revealed by drying the leaves after a term in the moist chamber.

Table 4. Simulated outcome of inoculation with 100 spores in moist chamber, 20 C, constantly wet, light and dark

Time		NUMBER	NUMBER	NUMBER	OPTY,	GSTK,	SPOR,
Day	Period	GERM,	NFECT,	DLSN,	MM^2	THSDS	THSDS
0	1	60	6				
	2	72	15				
	3	80	24				
	4		34				
	5		44				
	6		54				
	7		65				
	8		75				
1	1		78				
	2		80				
	....		....				
2	8			0	0		
3	1			75	0.2		
	2				2		
	3				3		
	....			....	....		
	8			75	11		
4	1			80	13[a]	2	
	2				15	5	
	3				17	12	2
	4				20	38	3
	5				22	67	8
	6				24	100	24
	7				26	136	42
	8				29	155	93
	....				....	....	....
6	8				58	297	250

---

[a] OPTY for DLSN(3).

As expected, the infections became visible after 3 days. These enlarged their area for stalks in the manner prescribed by Fig. 27 and the experiments incorporated in it. On the fourth day after infection, simulated stalks began to appear; this is consistent with Experiment 3/30A, where no stalks appeared in 3 days and where a few stalks appeared by the fourth day. Finally, simulated spores appeared on the fourth day, too; real spores were absent 3 days but present 4 days after the inoculation of Experiment 3/30A. Simulated spores continued to increase through days the fifth and sixth, as real ones had in Experiments 4/13, 20. Thus we end these calculations with the conclusion that EPIMAY adequately mimics the recognizable stages that follow inoculation of corn in a moist chamber and thereby passes her second test of realism.

The final test is simulating well known differences in natural epidemics of the past. Two cases provide tests. The second is the great southern corn leaf blight epidemic of 1970, an excellent test. The first or other test is somewhat contrived.

Helminthosporium turcicum is another fungus that blights corn. Although R. D. Berger has written that *H. turcicum* and *maydis* have different environmental requirements, it is interesting to learn how EPIMAY responds to Berger's (1970) forecasting rules for *H. turcicum* blight, which have proven successful for 3 years in Florida. He defines a Blight Favorable Hour (BFH) as having humidity near 100% and temperature above 15C. A daily average of 6.5 BFH causes too little blight to justify fungicide, while 11 BFH cause an epidemic regardless of fungicide. These forecasting rules are a summary of past epidemics of a closely related disease. Can EPIMAY duplicate their outcome?

The simulated epidemics for 7 days of 6, 9 or 12 BFH are set out in Table 5. Comparison of 12 and 9 BFH in the light shows the remarkably different outcomes of adding a third more BFH to 9 BFH: after 4 days there are nearly one and a half times as many new lesions, and by the end of a week the advantage — to *Helminthosporium* — has caused twice as many new lesions with 12 as with 9 BFH. The slower course of stalk formation in the dark causes the outcome of 9 BFH to be somewhat less disease if the BFH occur during the night rather than during the day. The effect of Berger's criterion of "warmer than 15C" is clearly seen in the fourth

Table 5. The simulated blight during 7 days when an initial 100 lesions are exposed to varying hours of Berger's Blight Favorable Hours during dark or light at 21 and 14 C

Hours BFH	Light	Temperature	New lesions on day 4	6	7	Accumulated new lesions
12	Light	21	34	15	132	181
9	Light	21	24	6	52	82
9	Dark	21	15	6	35	56
9[*]	—	14	0	0	0	0
6	—	21	0	0	0	0

[*] 9 hours wet, but too cool for BFH.

line of Table 5: at 14C the initial 100 lesions did not multiply because — as Fig. 6 shows — no stalks appear in 9 hours at 14C. Finally, 6 BFH permit no multiplication because — as Fig. 10 shows — no spores form on once-dried stalks after only 6 hours. Fresh or green stalks also provide no escape from the trap of 6 BFH: three 3-hour periods are required to form green stalks and then spores upon those stalks, Fig. 6 plus Fig. 8.

Berger (1970) reported another phenomenon that permits a comparison of simulation and reality. He collected about half the trapped spores in the 4 hours before noon, while only 5% were caught at night. If the simulated wind of our example is a steady 5 miles/hour, about a tenth of the spores are carried from stalks to air during every 3-hour period that is dry. Thus relative to the standing crop of spores the simulated air-borne spores during a wet and then succeeding dry periods would be: 0, 10, 9, 8, 7%, . . . A faster wind or a smaller stress UCON that removes half the spores would cause a faster decline in the air-borne spores. A continued 5-miles-per-hour wind but a UCON of only 100 would cause 54% of the spores flying in 15 hours to fly in the first 6 hours. Again, EPIMAY has proven realistic.

The final test of EPIMAY is in the epidemic of 1970. The maps of Moore (1970) showed blight as far north as Jackson, Tenn. on June 18 but no blight in central Georgia at the town of Experiment until after July 15. Accordingly weather data from Jackson and Georgia were introduced to EPIMAY along with an initial infection of 100 lesions. The outcome is shown in Fig. 28.

Clearly "a lack of moisture slowed development of the disease through . . . Georgia," while "one path (of blight) moved northward up the Mississippi River and surrounding areas . . ." (Moore, 1970). Moore's map shows a date of 6/13 north of Jackson. On that date the simulated lesions had increased 14 x 10^5 fold at Jackson, Tenn., but only 6 x 10^4 fold at Experiment, Ga. That is, according to EPIMAY the environment had been 20 times as favorable for blight at Jackson as in Georgia. Within a week, however, the simulated multiplication in Georgia had attained the June 13 level at Jackson. Given our ignorance of initial inoculum in real fields, the sketchiness of our knowledge of the epidemic, and the difficulties of splicing the weather and dew observations together, EPIMAY has performed moderately realistically.

Now, let us recur to the beginning of the section on "The realism of EPIMAY." We said that she could be employed confidently if three questions were answered favorably. In the intervening paragraphs we have found that the simulator has logical and measurable components, mimics a simple course of the fungus in a constant environment, and reproduces differences in epidemics of the past. Blemishes will surely be discovered in EPIMAY, but for now she seems passably realistic.

At the beginning of this section, we said that one of the purposes of a simulator was to distill a climatology of disease from a plethora of weather data. That is, the simulator and weather of years past can help estimate the probability of future disease if pathogen and host are unchanged.

Having the weather observations of Jackson and Georgia for 1969 as well as 1970 before us, we can make a modest beginning.

The courses of the simulated epidemics in the 2 years at the two places are described in Table 6 by the logarithms of the multiplication attained by the last days of May, June, July and August. Thus the initial lesions on May 1, 1969, in Georgia would have multiplied $10^{3.6}$ times by the end of May.

Two outcomes in Table 6 merit mention. First, the slow multiplication in Georgia in early 1970 is exceptional in this short list of examples. Second, multiplication in Tennessee during June through August 1969 was exceptionally slow. The conclusion from this brief climatology is that we cannot expect environment often to restrain blight as much as in Georgia in early 1970. On the other hand, a glimmer of hope rises from the fast simulated multiplication in Tennessee in 1970; perhaps the weather during the Great Epidemic was slightly more favorable than normal.

We cannot dispute the conclusion of Rahn and Barger (1970) that they reached after examining the weather of 1970. They did not have as much mycological information as in EPIMAY, but they examined more meteorological information than we have. Their conclusion was: "So the real problem remains. Over much of the corn producing area of North America chances are at least 1 in 2 that moisture will be sufficient to permit Southern Corn Leaf Blight in 1971." EPIMAY provides a tool for refining their climatology of disease, but the short beginning of Table 6 is ominous.

Connecticut has a surprisingly large acreage of the hybrid corn that began in Donald F. Jones' plots on the Lockwood Farm, Mt. Carmel. It is sweet corn for people and silage corn for cattle. What is the probability of this corn being blighted if it is susceptible to *H. maydis?*

Appropriately, the Mt. Carmel weather for 5 years and the Hartford weather for 1970 was introduced to EPIMAY. The 6 years set out in Table 7 include dry 1944, moist 1941 and 1950 and 1970, the year of the Epidemic. The dew for all 6 years was estimated from observations and notes by H. C. Engelhardt at the Lockwood Farm. The weather at Mt. Carmel is fairly representative of the entire state. Since Connecticut corn is planted later than the corn in Georgia and Tennessee, calculation was begun on June 1 rather than May 1. The probability of blight on T strain corn in Connecticut can be judged from Table 7, which shows the outcome of the simulations. It seems reasonable to compare the multiplication by the last day of July in the south, Table 6, to the multiplication by the last day of August in Connecticut, Table 7. Clearly the simulations for Connecticut

Table 6. Log_{10} of multiplication of *H. maydis* simulated by EPIMAY

Weather		Log_{10} of multiplication by last day of			
		MAY	JUN	JUL	AUG
1969	Georgia	3.6	8.7	14	20
	Tennessee	4.2	8.7	13	19
1970	Georgia	1.5	7.8	14	20
	Tennessee	3.8	9.4	15	21

Table 7. Log_{10} of multiplication of *H. maydis* simulated by EPIMAY for Mt. Carmel, Connecticut

Weather	Log_{10} of multiplication by last day of: JUN	JUL	AUG
1941	1.4	8.2	13
1943	3.1	9.2	14
1944	2.9	6.1	11
1950	4.9	10.4	16
1951	2.8	8.0	13
1970	3.2	9.0	16

bracket those for the southern station, telling us that the probability of blight in Connecticut is as great as in the regions ravaged by *H. maydis* in 1970. Likely the blight in Connecticut was slight in 1970 because of a scarcity of inoculum; but so far as the logic of the simulator can show us, we will have blight if the variety of corn is not changed from T type.

IV. EXPERIMENTS WITH THE CHARACTER OF PATHOGEN AND HOST

EPIMAY contains many characteristics of *Helminthosporium maydis* and even assumes something about the host, namely a constant susceptibility. If we alter these characteristics, a couple of purposes will be accomplished. First, the effectiveness or importance of the characters will be revealed. Second, where the numerical value of the character is uncertain, we shall see how susceptible our conclusions are to that uncertainty.

The outcome of a change in characters will be tested in 1970 weather of both Georgia and Tennessee. The experimenter in the outdoors has learned that one year's results are rarely like another, but the sheer cost of repetitious experimenting requires him sometimes to extrapolate from a single year. One of the virtues of EPIMAY is, of course, that the outcome in other years or places can be cheaply examined. Thus the effect of the changed characters are examined in both Georgia and Tennessee.

A. The Leaf Area

The leaf area LAI in cm^2 of leaf per cm^2 of land affects EPIMAY in two ways. It decreases the proportion of the spores washed into the AQUA account for a given rate of rainfall; once the area reaches 1, doubling the leaf area halves the rainfall rate. For example, when RM is .04 and rain falls at 0.10 inch/hour, the rule

$$\frac{\text{RAIN/LAI}}{\text{RM} + \text{RAIN/LAI}}$$

causes 72% of the spores to be suspended when LAI is 1 and 56% when LAI is 2.

Leaf area also affects aerial spread. First, leaves calm the wind and decrease the mean stress upon the spores for the same wind above the crop.

Second, the proportion of the air-borne spores that is caught was made proportional to the LAI.

Now let us examine the LAI that has been employed to now. LAI was caused to change on a parabola, Fig. 22, which was employed in EPIDEM. Since this parabola mimics potato leaf area, we must try the angular dashed curve of Fig. 22, which resembles the changes in leaf area observed by Allison (1969) and by Williams et al. (1969) when about 20 thousand corn plants were grown per acre.

The effects upon EPIMAY of the two rules for LAI were compared by simulating the development of blight for the first 50, critical days in Georgia and Tennessee. Three outcomes are tabulated in Table 8. First, the multiplication at Jackson in the 50 days was the antilogarithm of 7.2 when the parabolic rule was followed but only 6.9 or about half as great when the LAI increased along the angular curve.

The second outcome is the multiplication in Georgia relative to Jackson. Since the absolute numbers cannot yet be related to the proportion of leaves diseased or the decrease in yield, the relative multiplication is probably a more useful criterion than absolute multiplication at Jackson in 50 days. The relative multiplication in Georgia had a logarithm of —1.20 when the parabolic change in LAI was used, and —0.92 when the angular rule was followed. In other terms, the simulated disease in Georgia on the fiftieth day was 6% of that in Jackson by one rule for LAI, 12% by the other.

Finally, we calculated the multiplication at Jackson in the first 31 days, i.e. May, and asked how many more days were required in Georgia to reach this same level. The results were about the same by the two rules for LAI. Thus, given the inherent uncertainties in EPIMAY, the two rules for LAI are not greatly different in their outcomes although slightly more disease is simulated for the slightly greater LAI of the earlier rule. The angular course is used in subsequent calculation.

B. How the Pathogen is Blown and Caught

The greatest uncertainty concerns the spread of the pathogen on wind and rain. Wind disposal was characterized first by the stress UCON that would remove half the spores. To now we have assured that UCON is 200 or a wind of $(200)^{1/2}$ or 14 miles per hour will carry half the spores into the air. If UCON is dramatically reduced to 25, a wind of 5 miles per hour will carry away half the spores.

Two other parameters also affect aerial spread because the proportion caught was calculated as

$$(\mathrm{UCON2}/\mathrm{U}^{\mathrm{UPOW}}) * \mathrm{LAI}$$

To now UCON2 has been 2% and increasing it to 4% is reasonable. UPOW has been 0.5, reflecting a greater upward diffusion of spores than the increase in trapping efficiency with rising wind speed. Since Gregory (1961) could not discover a clear effect of wind on trapping efficiency, this relation is reasonable. However, it is also reasonable to remove this dependence on wind by making UPOW zero.

The former and varied values of the parameters for wind dispersal are:

UCON	200	25
UCON2	.02	.04
UPOW	.5	0

The changes cause the percentage of spores blown from an LAI of 1 and into the air by a 5-mile-per-hour wind to rise from 11 to 50% and by a 10-mile-per-hour wind to rise from 33 to 80%. The changes would cause the percentage of the air-borne spores that is caught to rise from 0.9 in a 5-mile-per-hour or 0.6 in a 10-mile-per-hour wind to a steady 4%.

The consequences of these changes in 50 days of 1970 weather at Jackson and Georgia are given in Table 8. Multiplication was greatly increased, and the disparity between Jackson and Georgia was also increased. Further, the time required for the disease in Georgia to reach the same level attained at Jackson on May 31 was increased markedly; this is not surprising since leaves were wet in Georgia 62% of the time during the first 11 days of June, preventing wind dispersal most of the time.

We have now examined what would happen if spores were more easily blown away and more frequently caught than first assumed. Since our first assumption was that fully a 14-mile-per-hour wind was required to cause half the spores to fly and that then fully 99.5% of the air-borne would escape our plot, there seems little need to examine changes in the opposite direction. Thus two conclusions seem safe.

First, the parameters affecting aerial dispersal have a great effect upon the cause of disease, and hence, absolute calculation of the progeny of a lesion is not safe until those parameters are better known. Endless refinement of other data, e.g. physiology, will not remove this major weakness. Second, despite this uncertainty, EPIMAY has considerable ability to mimic and hence explain the different epidemics of Jackson and Georgia.

V. EXHAUSTION OF THE HOST

Clearly the area of the lesions in a crop does not increase exponentially without limit; eventually the host is consumed, and spores have no new leaves to consume. Gregory (1948) has related to plant pathology Thompson's (1924) earlier analysis of the phenomenon of multiple infections and provided us with a logical means of introducing to EPIMAY the realism of an exhausted host.

Up to now we have allowed the simulated disease to increase without limit by making EXPO true in the namelist STARTS read on the first day. This is unrealistic but not without virtue. The virtue is that multiplication under that rule, as in Table 6 or 7, is solely a function of the weather. In other words, up to now the Fortran has translated weather complexities into a unique or single statement of the favorability of weather for *H. maydis*. As a final chapter in our Bulletin, however, we shall introduce the phenomenon of multiple infections or exhaustion of host, making EPIMAY that is less useful as an assay of the weather but an EPIMAY that is more realistic.

The heart of Thompson's analysis of multiple infections is that the probability of infection is proportional to the proportion of the host still healthy. In other terms, the increase Δy in disease caused by Δx pathogens landing on N hosts already afflicted by y disease is proportional to the ratio of (N-y) healthy to N total host:

$$\Delta y = \frac{N - y}{N} \Delta x$$

or in different form,

$$\frac{dy}{N - y} = \frac{dx}{N}$$

The solution of this equation is

$$y = N\ (1. - \exp(-x/N)),$$

which has been tabulated as the "multiple infection transformation" by Gregory. In EPIMAY, however, we calculate the increment Δy rather than the level of y disease. Thus we can consider the exhaustion of the host by simply multiplying the increment in CATCH by (N—y)/N, which we call PROB.

The task now is defining y and N. Earlier when we calculated the percentage of leaf area disease, we considered a 1 hectare (ha) field and the mm^2 of healthy and diseased leaves. The area of healthy leaves is

$$N = 10^4\ m^2/ha * 10^6\ mm^2/m^2 * LAI\ m^2/m^2$$

or the variable HECTAL. Since the area of diseased leaf is 3/2 of the stalk bearing area or OPTY, the diseased area in our little universe of the hectare is

$$3/2 \sum_{K=1}^{I} OPTY(K) * DLSN(K)$$

or the area of all the lesions appearing between days 1 and I. HECTAL and the sum of products of OPTY and DLSN are calculated near statement 83 as explained in Section II L.

In Georgia in 1970 the simulated lesions rose exponentially from 10^2 on day 1 to 2 X 10^8 on day 31 and on to 2 X 10^{11} on day 70. When grown to its maximum size, each lesion can occupy about 100 mm^2 (Fig. 20). The lesion area in mm^2 is, therefore, about 100 times the above numbers of lesions or 10^4, 2 X 10^{10}, and 2 X 10^{13} mm^2 on days 1, 31 and 70. Thus the probability (N—y)/N or PROB of landing on virgin territory is nearly 1 throughout the first month. During the second month, however, the proportion of the leaves diseased begins to climb significantly. Consequently, PROB begins to fall importantly, preventing the diseased area in the hectare from ever reaching the 2 X 10^{13} mm^2 of day 70 in the unrestricted EPIMAY. After all, on day 70 there are only 5 X 10^{11} mm^2 of leaves on the whole hectare! Instead of increasing without limit, the rate of increase in the modified EPIMAY is slowed and finally stopped by a falling probability PROB as the diseased area nears and finally reaches the total leaf area.

The reader will find the mechanism for considering tissue exhaustion has already been hidden in the Fortran. At the end of loop 99, i.e. at midnight, is a calculation of PROB. EXPO is a logical variable put into the STARTS card and read near statement 27 on the first day. It determines whether multiplication will be exponential or limited. Up to now EXPO has been true, PROB has been 1, increase has been exponential or unlimited, and the last statements in loop 99 have been skipped. Now, however, to consider host exhaustion we shall say EXPO is false, and PROB will be calculated from the lesion area TEMP and the total leaf area HECTAL on the hectare. In the section on dispersal after statement 39, the increment in CATCH from either aerial or aquatic dispersal is multiplied by PROB, which is no longer always 1.

The outcome for Georgia in 1970 is depicted in Fig. 29. On June 5 the lesion area finally reached a thousandth of the leaf area on the hectare, and PROB began to decline noticeably. By June 17 PROB was down to 88% because an eighth of the leaf area was diseased. Progress was then explosive: by June 25 the lesion area slightly exceeded leaf area, and the pathogen had nowhere to go. Thus in Fig. 29 one sees the curve PROB declines from nearly 100 percent to zero between June 15 and 25, and the curves for EXPOnential multiplication and multiplication limited by tissue EXHAUSTion take their separate courses from about June 30 onward.

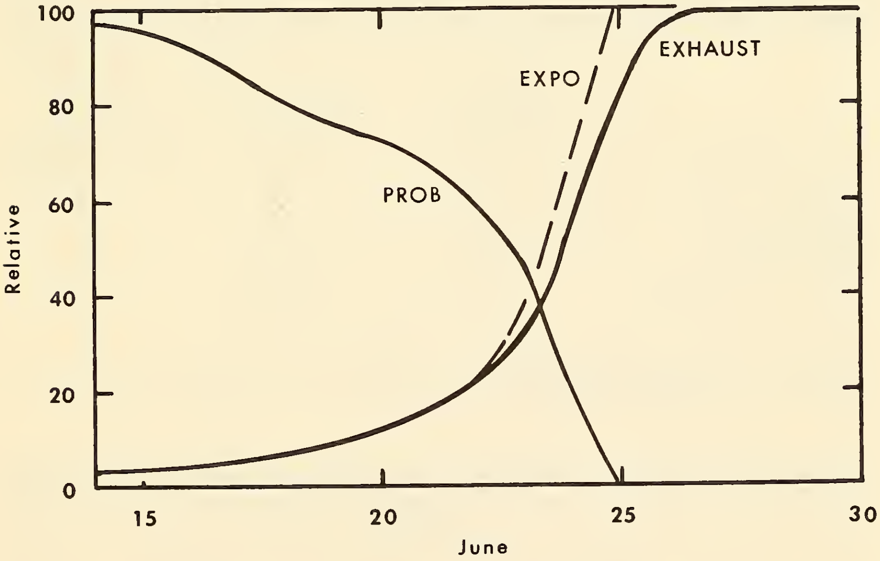


Fig. 29. Effect of an exhaustion of the host, Jackson 1970. Curve EXPO shows the exponential increase in simulated disease when host is unlimited. When leaf area is limited the PROBability of a spore alighting on healthy tissue declines noticeably after June 15 until it reaches zero on Jun 25, causing the disease simulated under the rules of EXHAUSTion of the host to cease rising. The ordinate is the relative logarithm of lesion multiplication or the probability.

The uncertainty in the parameters describing dispersal has often been mentioned in this Bulletin as the greatest difficulty in the entire simulator. As long as the parameters were kept constant and we were comparing one place or time with another, however, the outcome was not greatly affected. That is, Table 8 demonstrated that the relative severity of disease at Jackson and Georgia was not greatly altered by considerable changes in the parameters for dispersal. Now that we are considering the exhaustion of the leaf area, which is an absolute rather than relative number, the size of the parameters and the different absolute number of lesions that are calculated from them become very important. Therefore, the effect of different values is re-examined.

UCON2 decreases with the proportion of air-borne spores that is carried beyond the field and with the proportion of them that is ineffective. WASP decreases with the proportion of spores that is washed to the ground and the proportion of spores awash that is ineffective. These parameters are akin to the "infection efficiency" that Gregory (1961) found was a small percentage. Until now UCON2 has been 2% and WASP has been 5%. Table 9 shows the effect of decreasing these two upon the onset of disease.

The simulation for Georgia with the standard values of UCON2 and WASP is shown in the first line of the table. As written above and depicted in Fig. 29, blight occupied 0.1% of the leaves on June 5 or day 36. The

Table 8. The disease simulated for 50 days of 1970 weather at Jackson, Tennessee and in Georgia for several variations in fungal and host characteristics

Variation	$\log_{10}$ of multiplication at Jackson	$\log_{10}$ of relative multiplication in Georgia	Days in Georgia to reach May 31 level at Jackson
Parabolic LAI[a]	7.2	—1.2	7
Angular LAI	6.9	—0.9	6
Wind dispersal	11.0	—2.9	11
Rain dispersal	8.7	—1.2	5
Sun and susceptibility	6.6	—0.8	5
Incubation period	6.2	—0.8	6

---

[a] The two courses of LAI are depicted in Fig. IV 1. The angular course of LAI is used in all lines but the first.

Table 9. The number of days for simulated disease to occupy 0.1, 10 and 100 percent of the leaves when the dispersal parameters UCON2 and WASP have their standard values or a half, quarter or tenth of the standard values. 1970 weather

		Percent		
Place	Parameters	0.1	10	100
Georgia	Standard	36	48	56
	Half	40	58	69
	Quarter	48	73	82
	Tenth	67	88	100
Jackson	Standard	29	42	49

percentage afflicted then rose to 10% on day 48 and 100% on day 56. The second line shows the outcome of halving, the third line the outcome of quartering, and the fourth line the outcome of cutting to a tenth the two parameters. As one would expect, decreasing the proportion of the spores that are successful in their trip both delays the appearance of 0.1 percent disease and protracts the time from 0.1 to 100 percent of the leaves diseased.

This shows, as we expected, that the dispersal parameters must be known much more precisely than we now know them before we can realistically simulate *absolute* levels of disease.

Now how does the limit of host exhaustion rather than the unlimited multiplication formerly assumed affect the outcome in Jackson? This calculation is summarized on the last line of Table 9. The UCON2 and WASP have been restored to their standard values and this last line must be compared with the first line of the table. The simulated disease reaches the three levels of disease about a week earlier at Jackson than in Georgia. Thus, introducing the limit of host exhaustion does not change the realistic outcome of Fig. 28: simulated as well as real disease arrived earlier in Jackson than in central Georgia.

Three points need making at this time of conclusion. First, entering the limitation of host exhaustion makes the epidemic course a function of the level of disease as well as weather, and hence making EXPO false can make EPIMAY useless as an assay of the weather. Second, the limitation gives the epidemic course the negative feedback and upper limit that all real epidemics certainly have.

Finally and third, the rapidity of the increase from only 10 to fully 100 percent of the leaves diseased is startling. Thus in Georgia with the dispersal parameters at a tenth of their standard value, the blight required the 86 days up to July 24 to occupy 4% of the leaf area but by July 29 it had occupied 15%. In another 10 days it had fully involved the leaf area.

This explosive behavior is, of course, characteristic of real epidemics as testified by a letter from F. L. Crosby:

> "Dr. M. O. Jellum, corn breeder at (the Georgia Station), tells me that the first noticeable blight in his plots here in 1970 was on July 24th. His evaluation of the disease on that day showed . . . a small amount of disease was present. By July 29th, the susceptible lines were destroyed."

We end, therefore, by finding that this logical composition of laboratory observations and reasonable assumptions called EPIMAY provides an evaluation of the weather according to the tastes of *H. maydis* if EXPO is made true and a more realistic mimic of real epidemics if EXPO is made false.

SYMBOLS

AERIAL	Air-borne spores.
AQUA	Rain-borne spores.
AWASH	Fraction of spores washed away by rain.
BEATER	Proportion of stalks that survives the beating of a rain.
BFH	Blight favorable hours.
BLO	Proportion of spores blown from stalks.
CATCH	Number of dry spores resting on susceptible healthy leaves.
CENSUS	Subroutine for printing census.
CL(IC)	Relative susceptibility according to sun and hence photosynthesis of preceding day.
CSTK	Cold temperature that stops stalk formation, C.
DECAY	Decay of spores at rate F.
DETAIL	When true, details of calculation will be printed frequently.
DLSN(I)	Number of disease lesions that appeared on day I.
DRY	Leaves not wet.
DS	Increment in dry stalks DSTK per period.
DSTK(K)	Number of dry stalks (K=1) or dry stalks wetted (K-1) periods past.
DUM	Dummy variable.
DY(L)	Day of month of a rain.
ELAI	Leaf area index, cm^2 of leaf per cm^2 of land.
EXPO	When true, it causes disease to increase exponentially; when false, it causes disease to be limited by host exhaustion.
F	Function of dry spores that survives a 3-hour period.
FSTK	Number of fertile stalks, which equals SPOR.
GERM(K)	Number of spores germinated (K-1) periods past.
GRATE	Function subprogram for integration, finding the maximum or interpolation on a curve L.
GS	Increment in green stalks GSTK per period.
GSTK(K)	Number of green, i.e. never dried, stalks formed (K-1) periods past.
HECTAL	Leaf area in mm^2 per hectare.
HSTK	Hot temperature that stops stalk formation, C.
I	Subscript for current day.
IBEAT	Rate of rain that destroys half the stalks, inches/hr.
IBGN	Days after May or June 1.
IC	Subscript for CL that is 1 when both, 2 when one and 3 when neither past midday period is sunny.
ICBT	Number of days from infection or penetration to appearance of lesion.
IDSP(K)	Index of sporulation on dry stalks wet (K-1) periods ago.
IEND	Number of days of calculation.
IGLS(I)	Index of green stalk formation on lesions that appeared on day I.

IGM(K)	Index of penetration by spores germinated K-1 periods ago.
IGSP(K)	Index of sporulation on green stalks formed K periods ago.
IHR(L)	Initial hour of a rain.
IWC(K)	Index of germination of spores wetted K-1 periods ago.
J	Subscript for current 3-hour period.
K	Subscript for past day or past period.
L	Subscript.
LAI	Leaf area index. Equals ELAI.
LIT	Daylight.
M	Subscript.
N	Hosts.
NCBT(I)	Number of incubating infections of day I.
NFECT	Number of infections in current day.
NHR(L)	Last hour of a rain.
OPTY(I)	Area of lesions that appeared on day I, mm^2.
PROB	The probability of a spore landing on healthy rather than diseased leaves.
QTY(L)	Rain falling between IHR and NHR on DY(L) of month MO, inches.
RAIN(I,J)	Rate of rain on day I at period J, inches/hr.
RH(I,J)	Relative humidity on day I at period J.
RL	Product of LAI and RM, inches of rain/hr that remove half the spores from stalks.
RM	Inches of rain/hour per LAI that remove half the spores from stalks.
RP	Fraction of spores washed from stalks and caught each period when 0.01 inch/hour rain falls.
RPOW	100 times rain in inches/hr.
S(I,J)	Sun on day I at period J.
SPOR	Number of spores on stalks.
SPORI	Increase in SPOR
STALK	Subroutine for calculating new account GSTK.
STARTS	Namelist of initial conditions.
T(I,J)	Temperature on day I at period J, read in F and then converted to C. TNOW = T(I,J).
TAU	Mean wind stress in canopy, $(\text{miles/hr})^2$.
TEMP	Temporary variable of all work in Fortran. Temperature in flow chart.
TNOW	Temperature now. Equals T(I,J).
U(I,J)	Wind on day I during period J, miles/hour.
UCON	Wind stress that removes half the spores, $(\text{miles/hour})^2$.
UCON2	Incorporates the effects of field size, maximum leaf area index (LAI) loss of spores from the field upon the catching of air-borne spores on leaves. Dimensions of $(\text{miles/hour})^{-UPOW}$.

UPOW	Incorporates the effect of windspeed upon the catching of air-borne spores.
W(I,J)	Leaves wet on day I at period J.
WASH	Fraction of spores washed not away by rain.
WASP	Infective fraction of spores that are washed and caught.
WCATCH(K)	Number of spores caught on hosts that were wet (K-1) periods past.
WIND	Wind, miles/hour. Equals W(I,J).
WET	Leaves wet. Equals W(I,J).
WP(K)	Leaves wet K periods ago.
WXTIT	Title for weather data.
X	Time in 3-hour periods or in days in subprogram GRATE. Also pathogen level.
XSIZE	Maximum opportunity in mm^2 for stalk formation for current temperature.
Y	Response in subprogram GRATE. Also disease level.
ΔX	Increase in pathogens.
ΔY	Increase in disease.

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APPENDIX

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C EPIDEM MAYDIS SIMULATES SOUTHERN CORN LEAF BLIGHT.
C WRITTEN FROM OBSERVATIONS OF HELMINTHOSPORIUM MAYDIS IN LABORATORY
C OF CONNECTICUT AGRICULTURAL EXPERIMENT STATION, NEW HAVEN.
C OBSERVATIONS BY J G HORSFALL, R J LUKENS, BARBARA WOODING.
C PROGRAM BY P E WAGGONER. 4/12 TO 5/10/71. MODIFIED 5/25,28,7/13/71
C PROGRAM EDITED FOR PUBLICATION 2/14/72.
C PROGRAM CONSISTS OF MAIN, SUBROUTINE CENSUS AND FUNCTION GRATE.

       INTEGER DY(7),IHR(7), NHR(8)
       REAL T(125,8),RH(125,8),U(125,8),RAIN(125,8),CL(3),
      1DLSN(125),NCBT(125),IGLS(125),GSTK(16),DSTK(16),GERM(16),
      2WCATCH(16),IGSP(16),IDSP(16),IWC(16),IGM(16),NFECT,OPTY(125),
      3TITLE(16),WXTIT(16),QTY(7),IBEAT,END
       LOGICAL S(125,8),W(125,8),WP(16),DETAIL,LIT,EXPO
       COMMON OPTY,WCATCH,CATCH,IGLS,GSTK,GERM,NFECT,DSTK,SPOR
       DATA END/1HZ/,REPEAT/5HREPEA/,
      1START,STOKK,BEAT,SPORS,SPRED,GRM,INFCT,MDT/5HSTART,
      25HSTALK,4HBEAT,5HSPORS,5HSPRED,4HGERM,6HINFECT,3HMDT/
       NAMELIST/FUNGUS/UCON,UCON2,RM,UPOW,RP,WASP,ICBT,F,IBEAT,CSTK,HSTK
      1,CL/STARTS/DLSN1,CATCH,WP,IC,DETAIL,EXPO

C *** A. READING THE WEATHER REPORTS ***
C WXTIT IS TITLE FOR WEATHER. IBGN IS DAYS AFTER MAY 1 OR JUNE 1 FOR START.
 101   READ(5,1)WXTIT,IBGN
 1     FORMAT(16A5,T79,I2)
C A WXTIT(LE) OF -REPEAT- CAUSES REPETITION OF SAME WEATHER DATA,
C WHILE NEW FUNGAL CHARACTER IS READ.
       IF(WXTIT(1).EQ.REPEAT)GO TO 107
C A WXTIT(LE) OF -END- WHICH IS A Z STOPS CALCULATION.
       IF(WXTIT(1).EQ.END) STOP
       WRITE(6,2) WXTIT,IBGN
 2     FORMAT (-1-,T25,16A5,-   IBGN-, I3)

C READ DAILY TEMP,RH,WIND,SUN,WET CARD ENDED WITH Z CARD.
C BEGIN READING WEATHER ON MAY 1 PLUS IBGN DAYS.
       DO 3 I = 1,125
      READ(5,4)FIN,(T(I,J),RH(I,J),U(I,J),S(I,J),W(I,J),J=1,8)
 4    FORMAT(A1,3X,4(1X, 3F2.0,2L1),4(2X,3F2.0,2L1))
      IF(FIN.EQ.END) GO TO 5
 3    CONTINUE
 5    I=I-1
C NUMBER OF DAYS OF WEATHER READ IN IS COUNTED AND CALLED IEND.
      IEND=I

C CONVERT WX BUREAU-S FAHRENHEIT TO CELSIUS AND ZERO RAIN ACCOUNTS.
      DO 10 I=1,IEND
      DO 10 J=1,8
      T(I,J)=(T(I,J)-32.)*.5555
 10   RAIN(I,J)=0.0
C AFTER ZEROING ALL RAIN, READ ONLY OCCASIONS OF RAIN.
C QTY IN HDRDS INCH BETWEEN IHR AND NHR ON DAY L OF MONTH MO.
C SEVEN STORMS PER CARD.
      DO 11 K=1,25
      READ(5,12) MO,(DY(L),IHR(L),NHR(L),QTY(L),L=1,7)
 12   FORMAT(T3,I2,7(1X,3I2 ,F3.2))
C STOP READING RAIN CARDS WHEN BLANK REACHED.
      IF(QTY(1).EQ.0.0) GO TO 14
C CONVERT MONTH NUMBER TO NUMBER THAT CAN BE ADDED TO DATE FOR DAYS I.
      MO=(MO-5)*31
      IF(MO.GT.31)MO=MO-1
      DO 13 L=1,7
      IF(QTY(L).EQ.0.0) GO TO 11
      I=MO+DY(L)-IBGN
C CHANGE QTY PER STORM TO RAIN INCHES PER HOUR.
      JB=IHR(L)/3+1
      JE=NHR(L)/3+1
      IF(JE.GT.8)JE=8
      TEMP=NHR(L)-IHR(L)+1
      TEMP=QTY(L)/TEMP
      DO 13 J=JB,JE
      RAIN(I,J)=TEMP
 13   CONTINUE
```

```
      WRITE(6,76)I,JB,JE,TEMP,RAIN(I,JB),RAIN(I,JE)
 76   FORMAT(- -,3I3,3F10.3)
C SECOND ESTIMATE OF RAIN REPLACES FIRST.
C AFTER 7 STORMS REACH STATEMENT 11 AND READ NEW CARD.
 11   CONTINUE

C FOR CONSTANT SYNTHETIC CLIMATE READ ONE TEMP CARD AND ONE RAIN CARD.
C THIS EXEMPLARY DAY IS SPREAD THRU 7 DAYS HERE.
 14   IF(IEND.GT.1) GO TO 588
      IEND=7
      DO 587 I=1,IEND
      DO 587 J=1,8
      T(I,J)=T(1,J)
      RH(I,J)=RH(1,J)
      U(I,J)=U(1,J)
      S(I,J)=S(1,J)
      RAIN(I,J)=RAIN(1,J)
 587  W(I,J)=W(1,J)

C ASSURE WET LEAVES DURING RAIN. CHECK WX INPUT.
 588  DO 16 I=1,IEND
      DO 15 J=1,8
      IF(RAIN(I,J).GT..01) W(I,J)=.TRUE.
 15   CONTINUE
      WRITE(6,1016)I,(T(I,J),RH(I,J),U(I,J),RAIN(I,J),W(I,J),S(I,J),
     1J=1,8)
 1016 FORMAT(- -,I3,1X,4(3F4.0,F6.3,2L1)/T6,4(3F4.0,F6.3,2L1))
 16   CONTINUE
C DAILY ANALYSIS OF WEATHER IS WET, RAIN IN THSDTHS INCH/HR,
C RH AT PERIODS 7 AND 8 WHEN MOISTER THAN 83 PCT,
C BLIGHT FAVORABLE HOURS, SUNNY PERIODS, AND
C MEAN TEMP, RH, AND WIND.
      IIBFH=0
      IISUN=0
      TTBAR=0.0
      HHBAR=0.0
      UUBAR=0.0
      DO 500 I=1,IEND
      IBFH=0
      ISUN=0
      TBAR=0.0
      HBAR=0.0
      UBAR=0.0
      IRH=0
      IF(RH(I,7).GT.83.) IRH=RH(I,7)
      IIRH=0
      IF(RH(I,8).GT.83.)IIRH=RH(I,8)
      DO 568 J=1,8
      IF(W(I,J).AND.T(I,J).GE.15.)IBFH=IBFH+1
      IF(S(I,J))ISUN=ISUN+1
      TBAR=TBAR+T(I,J)
      HBAR=HBAR+RH(I,J)
      UBAR=UBAR+U(I,J)
  568 NHR(J)=RAIN(I,J)*1000.
      IIBFH=IBFH+IIBFH
      IISUN=IISUN+ISUN
      TTBAR=TTBAR+TBAR
      TBAR=TBAR/8.
      HHBAR=HHBAR+HBAR
      HBAR=HBAR/8.
      UUBAR=UUBAR+UBAR
      UBAR=UBAR/8.
  500 WRITE(6,509) I,(W(I,J),J=1,8),NHR,IRH,IIRH,IBFH,ISUN,TBAR,HBAR,
     1UBAR
  509 FORMAT(- -,I3,8L1,12I4,3F5.)
C SEASONAL SUMMARY OF 10*BFH PER DAY, 10*SUNNY PERIODS PER DAY AND
C MEAN TEMP, RH, AND WIND.
      IIBFH=(10*IIBFH)/IEND
      IISUN=(10*IISUN)/IEND
      TEMP=IEND
      TTBAR=TTBAR/TEMP/8.
      HHBAR=HHBAR/TEMP/8.
      UUBAR=UUBAR/TEMP/8.
      WRITE(6,510)IIBFH,IISUN,TTBAR,HHBAR,UUBAR
 510  FORMAT(-0TEN TIMES MEAN BFH AND SUNNY PERIODS PER DAY AND MEAN TEM
     CP RH AND WIND-/T10,2I4,3F5.1)

C *** B. FUNGAL CHARACTER ***
  107 READ(5,1) TITLE
      WRITE(6,200)TITLE
 200  FORMAT(-0-,T25,16A5)
C READ UCON, UCON2 AND UPOW CONCERNING WIND DISSEMINATION,
C RM, RP AND WASP CONCERNING RAIN DISSEMINATION,
C IBEAT CONCERNING BEATING OF STALKS BY RAIN,
C ICBT OR INCUBATION PERIOD IN DAYS, F OR NON-DECAYED SPORES AFTER 3 HOURS,
C CSTK AND HSTK OR COLD AND HOT TEMPERATURES THAT STOP STALK FORMATION.
      READ(5,FUNGUS)
      WRITE(6,FUNGUS)
C DAY I STARTS HERE.
      DO 99 I=1,IEND

C *** C. THE FIRST DAY ***
C SKIP TO STATEMENT 20 EXCEPT ON FIRST DAY.
      IF(I.NE.1) GO TO 20
C ZERO CUMULATIVE ACCOUNTS
      DO 17 J=1,IEND
      DLSN(J)=0.0
      IGLS(J)=0.0
      OPTY(J)=0.0
 17   CONTINUE
      SPOR=0.0
      DO 27 J=1,16
      WP(J)=.FALSE.
      DSTK(J)=0.0
      WCATCH(J)=0.0
      GERM(J)=0.0
      IGSP(J)=0.0
      IDSP(J)=0.0
      IWC(J)=0.0
      IGM(J)=0.0
 27   GSTK(J)=0.0
C STATUS AND HISTORY REQUIRED TO START.
C READ INITIAL LESIONS (DLSN1) CAUGHT SPORES (CATCH), PAST WET (WP)
C SUN INDEX FOR YESTERDAY (IC), AND WHETHER DETAIL OR EXPONENTIAL INCREASE.
      READ(5,STARTS)
      WRITE(6,STARTS)
      DLSN(1)=DLSN1
      PROB=1.
      CALL  CENSUS(START,1,1)

C AFTER FIRST DAY START DAY HERE. NFECT IS DAILY INFECTION AND BEGINS AT ZERO.
 20   NFECT=0.0
      IF(I.GT.10)DETAIL=.FALSE.
C IN EARLY VERSION OF EPIMAY, THE RULE FOR LEAF AREA WAS TAKEN FROM EPIDEM.
C LATER THIS WAS REPLACED BY A RULE MORE ACCURATE FOR MAIZE--
C INCREASE LAI FROM 2 ON DAY 1 ACCORDING TO ALLISON AND TO WILLIAMS ET AL.
      TEMP=I+IBGN
      ELAI=AMAX1(1.,GRATE(5,11,DUM,TEMP))
      RL=ELAI*RM

C 3 HOUR PERIOD STARTS HERE.
      DO 98 J=1,8
      IF(DETAIL)WRITE(6,25)I,J,T(I,J),RH(I,J),U(I,J),RAIN(I,J),S(I,J),
     1W(I,J),DLSN(I),ELAI,RL
 25   FORMAT(-UTIME-,2I3, - T,RH,U,RAIN,S,W-,3F5.0,F6.3,2L2,- DLSN-,
     1E10.3,- ELAI,RL-,2E10.3)
      TNOW=T(I,J)
      LIT=.TRUE.
      IF(J.LE.2.OR.J.GE.8)LIT=.FALSE.
C *** E. STALKS ARE FORMED ***
C NO STALK FORMATION ON DAY 1 OR ON DRY LEAVES.
      IF(I.EQ.1)GO TO 31
      IF(.NOT.W(I,J))GO TO 30
C IF WET, MOVE STALK ACCOUNTS AND SPORULATION INDICES.
```

```
      DO 29 KK=1,15
      K=16-KK
      GSTK(K+1)=GSTK(K)
      DSTK(K+1)=DSTK(K)
      IGSP(K+1)=IGSP(K)
      IDSP(K+1)=IDSP(K)
 29   CONTINUE
      GSTK(1)=0.0
      DSTK(1)=0.0
      IGSP(1)=0.0
      IDSP(1)=0.0
      IF(TNOW.LE.CSTK.OR.TNOW.GE.HSTK)GO TO 31
C L IDENTIFIES RELATION BETWEEN STALK FORMATION AND TIME FOR TEMP AND LITE STATE
      L=2
      IF(TNOW.GE.16.)L=4
      IF(TNOW.GE.21.)L=6
      IF(TNOW.GE.27.)L=8
      IF(TNOW.GE.33.)L=10
      IF(LIT)L=L-1
C KK IS DEVICE FOR SEARCHING FROM RECENT TO OLD DAYS K. K=1 IS YESTERDAY.
      NK=I-1
      DO 36 KK=1,NK
      K=NK-KK+1
C WHEN IGLS(K) GE 1 REACH 38 DIRECTLY AND DO NOT CHANGE GSTK OR IGLS.
      IF(IGLS(K).EQ.1.)GO TO 38
C CONTINUE TO K+1 IF NO OPTY ON K.
      IF(OPTY(K).EQ.0.)GO TO 36
      TEMP=IGLS(K)
C GRATE(1,L,IGLS(K),DUM) INCREASES IGLS ACCORDING TO SIZE OF IGLS.
      IGLS(K)=GRATE(1,L,TEMP,DUM)
C TEMP(ORARY) IS FORMER IGLS(K). CALCULATE GSTK(1) AFTER IGLS(K) IS INCREASED.
C OPTY(K) IS SQ MM FOR STALKS/DLSN(K).
C OPTY(K) OPENED DURING A WET PERIOD ARE TREATED AS IF OPEN FOR ENTIRE PERIOD.
C 300 IS MAX OPTY/SQ MM.
      GSTK(1)=GSTK(1)+(IGLS(K)-TEMP)*OPTY(K)*300.*DLSN(K)
 36   CONTINUE
```

```
      GO TO 38
C DRYING MAKES GSTK INTO DSTK(1), MOVES DSTK(K) TO DSTK(1), ZEROES INDICES.
 30   DO 44 K=1,16
      DSTK(1)=DSTK(1)+GSTK(K)
      IF(K.NE.1)DSTK(1)=DSTK(1)+DSTK(K)
      IF(K.NE.1)DSTK(K)=0.0
      IDSP(K)=0.0
      IGSP(K)=0.0
 44   GSTK(K)=0.0
 38   IF(DETAIL)CALL CENSUS(STOKK,I,J)
C RAIN DESTROYS SOME STALKS AND THUS OPTY TOO.
 31   IF(RAIN(I,J).EQ.0.)GO TO 35
      BEATER=IBEAT/(IBEAT+RAIN(I,J))
      DO 34 K=1,16
      GSTK(K)=GSTK(K)*BEATER
 34   DSTK(K)=DSTK(K)*BEATER
      IF(DETAIL)CALL CENSUS(BEAT,I,J)
C *** F. SPORES APPEAR ***
 35   SPORI=0.0
C NO SPORULATION IN DRY.
      IF(.NOT.W(I,J))GO TO 39
C HOT OR COLD PREVENTS SPORES
      IF(TNOW.GE.33..OR.TNOW.GE.27..AND.LIT.OR.TNOW.LE.4.)GO TO 39
C SELECT SPOR-TIME CURVE ACCORDING TO LIGHT AND TEMPERATURE.
C L FOR DSTK AND K FOR GSTK CURVE.
      L=31
      IF(TNOW.GE.16.)L=33
      IF(TNOW.GE.21.)L=35
      IF(TNOW.GE.27.)L=37
      IF(LIT)L=L-1
      K=13
      IF(LIT)K=12
      DO 45 M=2,15
      DS=0.0
      GS=0.0
C WP(1) PERMITS SPOR ON STK(3) FORMED 6 HRS AGO. REACHED WHEN M=2.
      IF(.NOT.WP(M-1))GO TO 39
      IF(DSTK(M+1).EQ.0.)GO TO 32
      TEMP=IDSP(M+1)
C GRATE(1,L,TEMP,DUM) INCREASES IDSP ACCORDING TO SIZE OF IDSP.
      IDSP(M+1)=GRATE(1,L,TEMP,DUM)
      DS=AMIN1((IDSP(M+1)-TEMP)/(1.-TEMP),1.)*DSTK(M+1)
 32   IF(GSTK(M+1).EQ.0.) GO TO 33
      TEMP=IGSP(M+1)
C GSTK FORM MAX SPORS ALLOWED BY TEMP AND LIGHT IN PERIOD WP(1), NONE BEFORE.
      TEMP2=GRATE(5,K,DUM,TNOW)
      IF(TEMP2.LE.TEMP)GO TO 33
      IGSP(M+1)=TEMP2
      GS=AMIN1((IGSP(M+1)-TEMP)/(1.-TEMP),1.)*GSTK(M+1)
 33   IF(DS.LE.0..AND.GS.LE.0.)GO TO 45
      SPORI=SPORI+GS+DS
      IF(DETAIL)WRITE(6,320)M,L,IDSP(M+1),TEMP,DSTK(M+1),IGSP(M+1),
     1GSTK(M+1),DS,GS,SPORI
 320  FORMAT(- M,L,IDSP,TEMP,DSTK,IGSP,GSTK,DS,GS,SPORI-,2I3,8E10.3)
C DECREASE STALK ACCOUNTS
      DSTK(M+1)=DSTK(M+1)-DS
      GSTK(M+1)=GSTK(M+1)-GS
 45   CONTINUE
C FSTK IS OMITTED FROM FORTRAN SINCE IT EQUALS SPOR.
 39   IF(DETAIL)CALL CENSUS(SPORS,I,J)
C FRACTION (1.-F) OF SPORES DECAYS EACH 3 HOURS.
      SPOR=SPOR*F
      CATCH=CATCH*F
C *** G. SPORES ARE WASHED OFF STALKS BY RAIN AND CAUGHT BY LEAVES ***
      IF(RAIN(I,J).EQ.0.0) GO TO 59
C RL INCHES OF RAIN/HR WASHES HALF SPORES AWAY.
      AWASH=RAIN(I,J)/(RL+RAIN(I,J))
      WASH=(1.-AWASH)
      AQUA=SPOR*AWASH
C WASHING DECREASES SPOR, CATCH, WCATCH AND GERM ACCOUNTS.
      SPOR=SPOR*WASH
      CATCH=CATCH*WASH
      DO 52 K=1,16
      WCATCH(K)=WCATCH(K)*WASH
 52   GERM(K)=GERM(K)*WASH
C FRACTION RP OF SPORES AWASH IS CAUGHT IN .01 INCH/HR RAIN FOR 3 HRS.
C FRACTION WASP OF WASHED AND CAUGHT SPORES IS EFFECTIVE.
      RPOW=RAIN(I,J)*100.
      CATCH=CATCH+AQUA*WASP*RP**RPOW*PROB
C ASSUME WASHED STALKS MUST ENTER DSTK(1) FOR SLOW SPORULATION.
      DSTK(1)=DSTK(1)+AQUA
      GO TO 60

C *** H. SPORES ARE BLOWN BY WIND AND CAUGHT BY LEAVES ***
C CALM OR WET LEAVES PREVENT SPREAD ON WIND.
 59   IF (W(I,J).OR.U(I,J).LT.1.) GO TO 60
C CALCULATE STRESS EACH LEAF AREA UNIT ACCORDING TO
C LN(U/U TOP)=0.7*ACCUMULATED LEAF AREA.
C CUT SPOR CROP BY STRESS TAU. UCON IS SQ OF MPH THAT REMOVES HALF SPORS.
C MEAN STRESS CALCULATED FROM U**2 BY INTERPOL ON CURVE 14 ACCORDING TO ELAI.
      TAU=U(I,J)**2*GRATE(5,14,DUM,ELAI)
      BLO=TAU/(TAU+UCON)
      AERIAL=SPOR*BLO
C BLO DECREASES SPORS ON STALKS
      SPOR=SPOR*(1.-BLO)
C BLOWN STALKS MUST ENTER DSTK(1) FOR SLOW SPORULATION.
      DSTK(1)=DSTK(1)+AERIAL
C CATCH INCREASES WITH ELAI AND DECREASES WITH WIND TO POWER UPOW.
C UCON2 IS FRACTION OF AIR-BORNE SPORES CAUGHT IN 1 MPH AND 1 LAI.
      CATCH=CATCH+AERIAL*ELAI/U(I,J)**UPOW*UCON2*PROB
      IF(DETAIL)WRITE(6,591)U(I,J),TAU,BLO,AERIAL
 591  FORMAT(- BLOW-,4E10.3)
 60   IF (DETAIL) CALL CENSUS(SPRED,I,J)
      SPOR=SPOR+SPORI
C *** I. SPORES GERMINATE ***
C GERM(K) ARE GERM IN PERIOD K. GERM(1) ARE GERM NOW.
C WCATCH(K) ARE WET IN PERIOD K. WCATCH(1) ARE CAUGHT ANYTIME, WET NOW.
C SPORES MAY BE CAUGHT, WET AND GERMINATED IN ONE PERIOD.
      IF(.NOT.W(I,J))GO TO 65
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C MOVE CATCH INTO WCATCH(1) BECAUSE NOW WET. MOVE GERM AND IGM ALSO.
      DO 61 KK=1,15
      K=16-KK
      IGM(K+1)=IGM(K)
      IWC(K+1)=IWC(K)
      GERM(K+1)=GERM(K)
 61   WCATCH(K+1)=WCATCH(K)
      IWC(1)=0.
      WCATCH(1)=CATCH
      CATCH=0.
      IGM(1)=0.
      GERM(1)=0.
C SELECT TIME-GERM CURVE ACCORDING TO TEMP.
      IF(TNOW.LE.5..OR.TNOW.GE.40.)GO TO 70
      L=22
      IF(TNOW.GE.12.)L=23
      IF(TNOW.GE.16.)L=24
      DO 62 M=1,16
C M CONTINUOUS WET PERIODS, WP + PRESENT. PRESENT M=1 PERMITS GERM.
      IF(M.EQ.1)GO TO 64
      IF(.NOT.WP(M-1))GO TO 70
C IWC(M) IS INDEX OF GERM OF CAUGHT SPORES WET M-1 PERIODS AGO.
C IWC CANNOT EXCEED 1.
C IWC INCREASES REGULARLY WITH AGE SINCE ALL OLDER THAN M EXPOSED TO
C M PLUS M+1 WEATHER.
C SINCE WCATCH(1) CAN RECEIVE MORE SPORES DURING WET PERIOD-
C -UNLIKE OPTY(K.NE.I)--USE WCATCH(M) MOVED TO M FOR EACH PAST WET PERIOD.
 64   IF(IWC(M).GE.1.)GO TO 70
C NO INCREMENT IN GERM IF WCATCH(M)=0, BUT SEARCH OLDER WCATCH.
      IF(WCATCH(M).LE.0.)GO TO 62
      TEMP=IWC(M)
C GRATE(1,L,IWC(M),DUM) CALCULATES NEW IWC ACCORDING TO SIZE OF IWC.
      IWC(M)=GRATE(1,L,IWC(M),DUM)
      IF(DETAIL)WRITE(6,68)J,M,TEMP,IWC(M),WCATCH(M),GERM(1)
 68   FORMAT(- J,M,TEMP,IWC(M),WCATCH(M),GERM(1)-,2I3,4F10.3)
      GERM(1)=GERM(1)+WCATCH(M)*(IWC(M)-TEMP)
 62    CONTINUE
       GO TO 70
C REACH THIS STATEMENT DIRECTLY IF LEAVES ARE DRY.
 65    DO 67 K=1,16
       WCATCH(K)=0.
 67    GERM(K)=0.
 70    IF(DETAIL)CALL CENSUS(GRM,I,J)
C *** J. GERMINATED SPORES INVADE LEAVES ***
C PENETRATION IMPOSSIBLE WHEN LEAVES ARE DRY.
       IF(.NOT.W(I,J)) GO TO 75
C SELECT TIME-FECT CURVE ACCORDING TO TEMPERATURE.
       IF(TNOW.GE.35..OR.TNOW.LE.10.)GO TO 75
       L=27
       IF(TNOW.GE.14.)L=28
       IF(TNOW.GE.32.)L=29
C GERM(NOW)=GERM(1) CAN INFECT IN SAME 3 HR PERIOD. EXP 3/16-17.
       DO 71 M=1,16
       IF(M.EQ.1)GO TO 72
       IF(.NOT.WP(M-1))GO TO 75
 72    IF(IGM(M).GE.1.)GO TO 75
       IF(GERM(M).LE.0.) GO TO 71
       TEMP=IGM(M)
       IGM(M)=GRATE(1,L,IGM(M),DUM)
 74    FORMAT(- J,M,TEMP,IGM(M),GERM(M),NFECT -, 2I3,5E10.3)
       NFECT=NFECT+GERM(M)*(IGM(M)-TEMP)*CL(IC)
       IF(DETAIL)WRITE(6,74)J,M,TEMP,IGM(M),GERM(M),NFECT,TNOW
 71    CONTINUE
 75    IF(DETAIL)CALL CENSUS(INFCT,I,J)

C *** L. LESIONS ENLARGE ***
C OPTY(K) IS INCREASED EACH 3 HRS.
       IF(TNOW.LE.10..OR.TNOW.GE.40.)GO TO 82
C SELECT OPTY-TIME CURVE ACCORDING TO TEMPERATURE.
       L=15
       IF(TNOW.GE.15.)L=16
       IF(TNOW.GE.21.)L=17
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      IF(TNOW.GE.33.)L=15
C XSIZE IS MAX OPTY ALLOWED BY CURVE L FOR TNOW.
      XSIZE=GRATE(4,L,DUM,DUM)
      DO 81 KM=1,I
      K=I-KM+1
      IF(OPTY(K).GE.XSIZE)GO TO 82
      IF(DLSN(K).LE.0.)GO TO 81
      TEMP=OPTY(K)
C INCREASE OPTY(K) ACCORDING TO OPTY ACHIEVED AND TO TEMPERATURE.
      OPTY(K)=GRATE(1,L,TEMP,DUM)
      IF(DETAIL)WRITE(6,812)K,L,DLSN(K),TEMP,OPTY(K),XSIZE
 812  FORMAT(- K,L,DLSN(K),TEMP,OPTY(K),XSIZE-,2I3,4E10.3)
 81   CONTINUE
C EACH 3 HRS MOVE W(ET) P(AST) ACCOUNTS INTO PAST.
 82   DO 23 KK=1,15
      K=16-KK
 23   WP(K+1)=WP(K)
      WP(1)=W(I,J)
 98   CONTINUE
C 3-HOUR PERIOD J ENDS HERE.
C *** K. INFECTIONS INCUBATE ***
C AT MDT DUMP NFECT INTO INCUBATION NCBT, TAKE NCBT(ITT) FROM INCUBATION.
C NCBT(I) IS INFECTION ON DAY I ONLY.
      NCBT(I)=NFECT
C DLSN(I+1) IS NOT CUMULATIVE, I.E. IT IS ONLY NEW LESIONS ON DAY I+1.
      ITT=I-ICBT+1
      IF(ITT.LT.1)DLSN(I+1)=0.0
      IF(ITT.GE.1)DLSN(I+1)=NCBT(ITT)
C IC INDICATES CLOUDINESS OF MIDDAY.
C CLOUDY NONE 10-OR-13 10-AND-13 HOURS
C   IC    1      2         3
      IC=3
      IF(S(I,4).OR.S(I,5))IC=2
      IF(S(I,4).AND.S(I,5))IC=1
      IF(DETAIL)WRITE(6,771)NFECT,(NCBT(K),DLSN(K),K=1,I)
 771  FORMAT(- -,10E10.3)
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      IF(DETAIL)WRITE(6,772)S(I,4),S(I,5),IC
 772  FORMAT(- -,2L1,I2)
      IF(DETAIL)CALL CENSUS(MDT,I,J)

C THIS SECTION CONCERNS AREA OF DISEASED LEAVES AND PROBABILITY OF CATCH ON
C HEALTHY AREA OF LEAF.
      IF(DETAIL.AND.I.NE.IEND)WRITE(6,77)
 77   FORMAT(-1-)
C TEMP IS AREA OF DISEASED LEAF TISSUE, WHICH IS 1.5 TIMES OPTY.
      TEMP=0.0
      DO 83 K=1,I
 83   TEMP=TEMP+OPTY(K)*DLSN(K)*1.5
C HECTAL IS SQ MM OF HEALTHY PLUS DISEASED LEAVES PER HECTARE.
      HECTAL=ELAI*1.0E10
C PCT IS PERCENTAGE OF LEAF AREA DISEASED.
      PCT=100.*TEMP/HECTAL
C EXPO IS TRUE IF EXPONENTIAL INCREASE OF DISEASE IS TO BE CALCULATED
C RATHER THAN INCREASE LIMITED BY SUPPLY OF HOST TISSUE.
C PROB IS PROBABILITY OF CATCH ON HEALTHY LEAF TISSUE, WHICH IS
C THE PROPORTION OF THE LEAF AREA THAT IS STILL HEALTHY.
      IF(.NOT.EXPO)PROB=AMAX1(0.0,(HECTAL-TEMP)/HECTAL)
      IF(I.EQ.1.OR.I.EQ.IEND)WRITE(6,1101)
 1101 FORMAT(T13,-I     NFECT       ELAI     HECTAL       TEMP        PCT
     1   PROB-)
      WRITE(6,999)I,NFECT,ELAI,HECTAL,TEMP,PCT,PROB
 999  FORMAT(T10,I4,6E10.3)
      IF(PROB.EQ.0.0)GO TO 110
 99   CONTINUE
C DAY I ENDS HERE.
C SUMMARY OF NEW LESIONS ON EACH DAY IS WRITTEN AT SEASON-S END.
 110  WRITE(6,109)WXTIT
 109  FORMAT(-1-,T25,16A5)
      WRITE(6,100)TITLE
  100 FORMAT(- -,T25,16A5/ T55,-NEW LESIONS-)
      WRITE(6,103)(K,K=1,10),(DLSN(K),K=1,IEND)
  103 FORMAT(- -,T4,I1,9I10/3(10E10.3/)E10.3//3(10E10.3/)/
     13(10E10.3/)E10.3// 4(10E10.3/))
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C CONVERT NEW LESIONS TO ACCUMULATED LESIONS WITH DLSN(1) AT LEAST 1.
      WRITE(6,102)
  102 FORMAT(- -,T55, -ACCUMULATED LESIONS-)
      DLSN(1)=AMAX1(1.,DLSN(1))
      DO 104 K=2,IEND
  104 DLSN(K)=DLSN(K-1)+DLSN(K)
      WRITE(6,103)(K,K=1,10),(DLSN(K),K=1,IEND)
C CONVERT ACCUMULATED LESIONS TO LOGARITHMS.
      DLSN(1)=ALOG10(DLSN(1))
      DO 106 K=2,IEND
  106 DLSN(K)=ALOG10(DLSN(K)) - DLSN(1)
      WRITE(6,108)
  108 FORMAT(- -,T55,-LOG MULTIPLICATION OF LESIONS-)
      WRITE(6,103)(K,K=1,10),(DLSN(K),K=1,IEND)
      GO TO 101

C DATA IS WXTITLE, WX, Z, RAIN, BLANK, $FUNGUS$, $STARTS$, AND
C THEN ANOTHER WXTITLE.
C IF WXTITLE SAYS REPEAT, WX AND RAIN CARDS SKIPPED. IF WXTITLE IS Z, STOP.
      END
      FUNCTION GRATE(K,L,YA,XA)
C GRATE PERFORMS DIFFERENT TASKS ACCOR4ING TO K.
C INTEGRATE THROUGH ONE 3-HR PERIOD ALONG  CURVE L TO NEW Y FROM
C ARGUMENT OLD Y (K=1) OR X (K=2).
C FIND INCREMENT FOR ONE 3-HR PERIOD ON CURVE L FROM ARGUMENT X (K=3).
C FIND MAX Y ON CURVE L (K=4).
C INTERPOLATE Y ON CURVE L FROM ARGUMENT X (K=5).
      REAL DLSN(125),OPTY(125),WCATCH(16),CATCH,IGLS(125),GSTK(16),GERM(
     116),NFECT,VNV,DSTK(16)       ,X(37,5),Y(37,5)
      COMMON OPTY,WCATCH,CATCH,IGLS,GSTK,GERM,NFECT,DSTK,SPOR
      DATA
CURVES 1-10 PERTAIN TO STALK-TIME FOR CERTAIN TEMP AND LITE.
     X((X(I,J),I=1,10),J=1,5)/10*0.,10*2.,10*8.,10*16.,10*24./,
     Y(Y(I,1),I=1,37)/10*0.0,0.5,2*0.0,1.0,23*0.0/,
     1(Y(1,J),J=2,5)/ 2*0.,.04,.08/,
     2(Y(2,J),J=2,5)/.00,.00,.15,.30/,(Y(3,J),J=2,5)/.01,.11,.26,.39/,
     3(Y(4,J),J=2,5)/.02,.22,.39,.50/,(Y(5,J),J=2,5)/.04,.44,.50,.50/,
     4(Y(6,J),J=2,5)/.02,.18,.43,.50/,(Y(7,J),J=2,5)/ .06,.63,.80,1.0/,
     5(Y(8,J),J=2,5)/.05,.50,.58,.60/,(Y(9,J),J=2,5)/.00,.00,.00,.00/,
     6(Y(10 ,J),J=2,5)/.02,.25,.25,.25/,
CURVE 11 IS ALLISON-S RELATION OF CORN LAI TO DAY.
     X(X(11,J),J=1,5)/1.0,42.0,70.0,112.0,140.0/,
     Y(Y(11,J),J=2,5)/    2.0,5.0,5.0,4.0/,
CURVES 12 AND 13 PERTAIN TO GSPOR-TEMP RELATION IN LIT AND DARK.
     X(X(12,J),X(13,J),J=1,5)/2*12.,2*18.,2*23.,2*30.,2*35./,
     Y(Y(12,J),Y(13,J),J=2,5)/.88,.94,.47,.94,.0,.58,2*0./,
CURVE 14 PERTAINS TO MEAN STRESS-ELAI RELATION
     X(X(14,J),J=1,5)/1.,1.5,2.,3.,4./,
     Y(Y(14,J),J=2,5)/.75,.62,.44,.33/
      DATA
CURVES 15-17 GIVE SQ MM OF LESION FOR STALK, I.E. OPTY.
     X((X(I,J),I=15,17),J=1,5)/3*0.,3*1.,3*8.,3*16.,3*24./,
     1(Y(15,J),Y(16,J),Y(17,J),J=2,5)/2*.06,.16,2*5.8,11.2,15.4,24.3,29.
     24,23.,37.1,57.6/,
CURVES 22-24 PERTAIN TO GERM-TIME ACCORDING TO TEMP.
     X((X(I,J),I=22,26),J=1,5)/5*0.,5*1.,5*2.,5*3.,5*8./,
     1(Y(22,J),J=2,5)/.00,.00,.05,.50/,(Y(23,J),J=2,5)/.30,.36,.40,.60/,
     2(Y(24,J),J=2,5)/.60,.72,.80,.80/,
CURVES 27-29 PERTAIN TO FECT-WET TIME  ACCORDING TO TEMP.
     X((X(I,J),I=27,29),J=1,5)/3*0.,3*1.,3*5.,3*8.,3*16./,
     1(Y(27,J),J=2,5)/.01,.01,.10,.10/,(Y(28,J),J=2,5)/.10,.60,1.,1./,
     2(Y(29,J),J=2,5)/.01,.01,.10,.10/,
CURVES 30-37 PERTAIN TO SPOR-WET TIME ACCORDING TO LITE AND TEMP.
     X((X(I,J),I=30,37),J=1,5)/8*0.,8*2.,8*8.,8*16.,8*24./,
     1((Y(I,J),I=30,37),J=2,5)/8*0., 2*0.,.73,.89,.17,.81,.00,.33
     2,.25,.10,.88,.94,.47,.97,.00,.58,.25,.10,.88,.94,.47,.97,.00,.58/
      X1=XA
      Y1=YA
C K=4 MEANS FIND MAX Y=Y(L,5)
      IF(K.EQ.4) GO TO 5
C K=5 MEANS INTERPOLATE Y FROM X1.
      IF(K.EQ.5)GO TO 6
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C Y CANNOT EXCEED Y(L,5)
      IF(Y1.GE.Y(L,5)) GO TO 3
C IF  X LT 0 AND USING X TO CHANGE Y, MAKE X=0
C FORCE X1 INTO RANGE OF X.
      IF(K.GE.2)X1=AMIN1(X1,X(L,5))
      IF(K.GE.2) X1=AMAX1(X1,0.)
C IF Y LT 0 AND USING Y TO CALCULATE INCREMENT IN Y, MAKE Y=0.
      IF(K.EQ.1)Y1=AMAX1(Y1,0.)
C K 1 SELECTS INTERVAL FROM Y, K 2 SELECTS IT FROM X
      DO 1 I=1,4
      IF(K.NE.1)GO TO 4
C SEARCH FOR Y INTERVAL IN MONOTONIC FUNCTION
      IF(Y1.GE.Y(L,I).AND.Y1.LT.Y(L,I+1))GO TO 2
      GO TO 1
 4    IF(X1.GT.X(L,I).AND.X1.LE.X(L,I+1))GO TO 2
 1    CONTINUE

C LOOP COMPLETED IF EXCESS X OR Y. IN THIS CASE, NO CHANGE IN Y.
 3    IF(K.NE.3)GRATE=Y1
      IF(K.EQ.3)GRATE=0.
      RETURN

C INTERPOLATE INCREMENT AND ADD TO Y1, BUT DO NOT EXCEED Y(L,5)
 2    IF(K.NE.3)GRATE=AMIN1(Y(L,5),
     1Y1+(Y(L,I+1)-Y(L,I))/(X(L,I+1)-X(L,I)))
C K=3 MEANS GET INCREMENT. Y1 IS ONLY DUMMY IN THIS CASE.
      IF(K.EQ.3)GRATE=(Y(L,I+1)-Y(L,I))/(X(L,I+1)-X(L,I))
      RETURN
C WHEN K=4 GET MAX Y.
 5    GRATE=Y(L,5)
      RETURN
C WHEN K=5 INTERPOLATE Y FROM X1.
C OUTLYING X BROUGHT INTO RANGE DEFINED
 6    X1=AMAX1(X1,X(L,1))
      X1=AMIN1(X1,X(L,5))
      DO 7 I=1,4
      IF(X1.GE.X(L,I).AND.X1.LT.X(L,I+1))GO TO 8
 7    CONTINUE
      GRATE=Y(L,5)
      RETURN
 8    GRATE =Y(L,I)+(Y(L,I+1)-Y(L,I))/(X(L,I+1)-X(L,I))*
     1(X1-X(L,I))
      RETURN
      END
      SUBROUTINE CENSUS(TITLE,I,J)
C SUBROUTINE CENSUS PERIODICALLY SHOWS STATUS IF -DETAIL- IS TRUE.
      REAL DLSN(125),OPTY(125),WCATCH(16),CATCH,IGLS(125),GSTK(16),GERM(
     116),NFECT,VNV,DSTK(16)
      COMMON OPTY,WCATCH,CATCH,IGLS,GSTK,GERM,NFECT,DSTK,SPOR
      DATA IJUN, IJUL, IAUG, IMAY/3HJUN,3HJUL,3HAUG,3HMAY/
      M=IMAY
      IF(I.GT.31)M=IJUN
      IF(I.GT.61)M=IJUL
      IF(I.GT.92)M=IAUG
      IDAY=I
      IF (M.EQ.IJUN)  IDAY=I-31
      IF (M.EQ.IJUL)  IDAY=I-61
      IF (M.EQ.IAUG)  IDAY=I-92
      IF(I.LE.2) GO TO 3
      LL=I-2
      K=I-1
      GO TO 4
 3    LL=1
      K=2
 4    WRITE(6,5)TITLE,M,IDAY,J
 5    FORMAT(-    -,A6,1X,A3,I4,- PERIOD-,I3 )
      WRITE(6,2)(OPTY(L),L=LL,K),(IGLS(L),L=LL,K),(GSTK(L),L=1,4),
     1(DSTK(L),L=1,4),SPOR,CATCH,(WCATCH(L),L=1,4),(GERM(L),L=1,4),NFECT
 2    FORMAT(- OPTY-,2E10.2,- IGLS-,2E10.2,- GSTK-,4E10.2/
     1- DSTK-,4E10.2, - SPOR ,CATCH-,2E10.2/
     2- WCATCH-,4E10.2,- GERM-,4E10.2, - NFECT-,E10.2)
      RETURN
      END
$DATA
```

ERRATA

Connecticut Agricultural Experiment Station
Bulletin 729, EPIMAY

Page	
24	Second line of legend, read "right-hand" for "lower."
40	Second line of second full paragraph, read "Fig. 23" for "Fig. 24."
41	Last line, read "reasonable" for "responsible."
56	Third line in Section B, read "assumed" for "assured."

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*** I. SPORES GERMINATE ***
GERM(K) ARE GERM IN PERIOD K. GERM(1) ARE GERM NOW.
WCATCH(K) ARE WET IN PERIOD K. WCATCH(1) ARE CAUGHT A
SPORES MAY BE CAUGHT, WET AND GERMINATED IN ONE PERIO
     IF(.NOT.W(I,J))GO TO 65
MOVE CATCH INTO WCATCH(1) BECAUSE NOW WET. MOVE GERM
     DO 61 KK=1,15
     K=16-KK
     IGM(K+1)=IGM(K)
     IWC(K+1)=IWC(K)
     GERM(K+1)=GERM(K)
61   WCATCH(K+1)=WCATCH(K)
     IWC(1)=0.
     WCATCH(1)=CATCH
     CATCH=0.
     IGM(1)=0.
     GERM(1)=0.
SELECT TIME-GERM CURVE ACCORDING TO TEMP.
     IF(TNOW.LE.5..OR.TNOW.GE.40.)GO TO 70
     L=22
     IF(TNOW.GE.12.)L=23
     IF(TNOW.GE.16.)L=24
     DO 62 M=1,16
M CONTINUOUS WET PERIODS. WP + PRESENT. PRESENT M=1 P
     IF(M.EQ.1)GO TO 64
     IF(.NOT.WP(M-1))GO TO 70
IWC(M) IS INDEX OF GERM OF CAUGHT SPORES WET M-1 PERI
IWC CANNOT EXCEED 1.
IWC INCREASES REGULARLY WITH AGE SINCE ALL OLDER THAN
M PLUS M+1 WEATHER.
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